Rapid Communication

Drought, disease, defoliation and death: forest pathogens as agents of past vegetation change

JQS

MARTYN WALLER[1]*
[1]Centre for Earth and Environmental Science Research, School of Geography, Geology and the Environment, Kingston University, Surrey, KT1 2EE, UK

ABSTRACT: The temperate and boreal forests of Europe and North America have been subject to repeated pathogen (fungal disease and phytophagus insect) outbreaks over the last 100 years. Palaeoecology can, potentially, offer a long-term perspective on such disturbance episodes, providing information on their triggers, frequency and impact. Mid-Holocene declines in *Tsuga* and *Ulmus* pollen dominate the Quaternary literature on forest pathogens, yet the role of pathogens, and even the presence of pathogenic fungal diseases, during these events has yet to be established. Pathogen-focused research strategies, informed by the sequence of events documented in modern outbreaks, and undertaken at high temporal resolution using a multi-proxy approach, are required. It is argued that forest pathogens are likely to have been significant agents of past vegetation change, even in cases where climate change was the primary stress factor. Copyright © 2013 John Wiley & Sons, Ltd.

KEYWORDS: climate change; disturbance; forest pathogens; Holocene; palaeoecology.

Introduction

A recently emerged invasive fungal disease is currently threatening populations of common ash (*Fraxinus excelsior* L.) across temperate Europe. Ash dieback, first recorded in Poland in the early 1990s (Husson *et al.*, 2011; Kraj *et al.*, 2012), had by 2010 been reported from 22 countries (Timmermann *et al.*, 2011). The causal agent appears to be a new species of ascomycete (*Hymenoscyphus pseudoalbidus* Roberge ex Desm.), a sexually reproducing form of the fungus *Chalara fraxinea* (T. Kowalski) (Kraj *et al.*, 2012). Ascospores, released from fallen leaves and twigs and dispersed by wind (Timmermann *et al.*, 2011), are thought to be the primary source of infection and responsible for the rapid spread of the disease, although the commercial trade in seedlings has also been implicated (Pautasso *et al.*, 2013). Seedling death often occurs within a few years, while in mature individuals the disease becomes chronic and the weakened trees vulnerable to attack by secondary pathogens, such as *Armillaria* (Timmermann *et al.*, 2011). The immediate outlook for ash, along with the biodiversity associated with this tree in Europe, is dismal. For example, it has been estimated that 60–90% of ash stands in Denmark are affected and likely to disappear (van Opstal, 2011).

The temperate and boreal forests of Europe and North America have been considerably altered by repeated outbreaks of fungal diseases over the last 100 years. Europe has seen the loss of alder and oak populations due to epidemics of various *Phytophthora* spp. (Jung *et al.*, 2000; Thomas *et al.*, 2002; Brasier *et al.*, 2004), while the forests of North America have experienced outbreaks of beech bark disease (*Neonectria coccinea* var. *faginata* Lohm.) and both continents have been affected by chestnut blight (*Cryphonectria parasitica* [Murr.] Barr) and Dutch elm disease (*Ophiostoma ulmi* [Buisman] Nannf. nd *O. novo-ulmi* Brasier) (Schlarbaum *et al.*, 1997; Sutherland *et al.*, 1997; Brasier and Buck, 2002). Wood-boring 'bark beetles' serve as vectors for beech bark disease and Dutch elm disease and insect larvae can also be

*Correspondence to: M. Waller, as above.
Email: m.waller@kingston.ac.uk

important agents of high intensity and large-scale disturbance events through defoliation. In North America the forest tent caterpillar (*Malacosoma disstria* Hübner) infected millions of hectares of sugar maple (*Acer saccharum* Marsh.) between 2002 and 2007 (Wood *et al.*, 2010), while eruptions of the gypsy moth (*Lymantria dispar* L.), introduced from Europe in the 19th century, may extend over thousands of hectares in any one year (Liebhold *et al.*, 2012).

Today fungal diseases and phytophagus insects (hereafter referred to as 'pathogens') are a major source of disturbance in temperate and boreal forest ecosystems and influence species diversity and distribution, structure and ecosystem function (e.g. Castello *et al.*, 1995; Holdenrieder *et al.*, 2004). Long-term records could make a significant contribution to a better understanding of certain aspects of such episodes, notably their triggers, recurrence interval and enduring impact. This article details the sedimentary evidence relating to past and conjectured past outbreaks and examines both how palaeoecological research might more effectively be used to document such outbreaks and the role of pathogens as agents of past vegetation change. First, the nature and causes of recent pathogen episodes are briefly reviewed.

Pathogens in the present

In addition to large-scale events, the activities of pathogens are perpetual within woodlands and responsible for weakening, as well as killing, individual or small groups of trees. They tend to be, but are not always, species-specific. Other species are indirectly influenced by changes in competition. Pathogenic fungi infect root, stem and foliar tissue. Trees weakened by age, shade or drought are particularly liable to attack, although fungi may also be primary agents of mortality. Defoliation by insects weakens trees through the depletion of carbohydrate reserves. With short life cycles and high reproductive potential, insect populations can fluctuate substantially. Some persist at low population densities and periodically expand to epidemic proportions, resulting in the total defoliation of host trees. The causes of the latter have been subject to much debate, but are considered influenced

by the populations of both generalist predators and species-specific pathogen/parasites of the insects (Dwyer *et al.*, 2004). Bark beetles comprise a diverse group of insects (Coleoptera, Curculionidae, Scolytidae) that feed largely on the phloem tissue of woody plants. Their attacks reduce growth and can be significant in causing mortality. Many interact with pathogenic fungi, targeting infected trees as well as acting as disease vectors.

A number of processes can cause infectious plant diseases, such as ash dieback, to emerge (Anderson *et al.*, 2004; Desprez-Loustau *et al.*, 2007). The geographical range of the pathogen can be extended. In these circumstances, the vulnerability of the host is likely to be high due to the absence of coevolution with the pathogen (Brasier and Buck, 2002). Pimentel *et al.* (2001) estimate that 65–85% of plant pathogens worldwide are exotic to the area where they are now found. Human activity, i.e. long-distance trade and the transport of specimens for planting, has been implicated in the spread of many plant pathogens. For example, chestnut blight is believed to have been introduced into the north-eastern USA on Asian chestnut trees in the late 19th or early 20th century (Pridnya *et al.*, 1996). A number of the more recent fungal outbreaks, including Dutch elm disease, evidence for which pre-dates the 20th century (Rackham, 2003), and ash dieback can be attributed to hybridization (Brasier, 2001; Husson *et al.*, 2011) which may allow a pathogen to escape previously effective defence mechanisms. Increased hybridization may also be a consequence of human activity, with greater mobility resulting in the co-occurrence of related, but previously allopatric, species.

Changes in the host and/or in the environment are a further major trigger for emerging plant diseases. The genetic diversity of the host influences the impact of the pathogen. For example, resistance to Dutch elm disease in Britain seems to be greater in *Ulmus glabra* (Huds.), which reproduces sexually and is therefore genetically diverse, in comparison with the more vulnerable *U. procera* (Salisb.), which reproduces clonally and may be a genetically unaltered Roman import (Gil *et al.*, 2004). Environmental change can impact directly upon the health of the host (e.g. the effects of drought on tree physiology) or upon the pathogen through effects on development and survival. The ability of some foliar disease fungi to produce spores and infect hosts is, for example, related to temperature and precipitation (e.g. Gadgil, 1977; Woods *et al.*, 2005). There is also the potential for climate to influence the spread of fungi though a series of plant–pathogen interactions from extending the range of vectors, to changing tree resistance by controlling nutrient availability.

When considering the role of pathogens in forest ecosystems it is useful to recognize that disturbance events often consist of a series of interactions between abiotic and biotic factors. Primary factors (climate or a pathogen), responsible for initial stress, weaken trees which, with their resistance compromised, are then vulnerable to secondary factors (bark beetles, fungal diseases) which can continue attacking trees even if the primary factor is no longer active (Table 1). Death, accompanied by saprophytic colonizers, can occur many years later. The affected area, after a time lag of a number of years, may then be vulnerable to fire because of an increase in the amount of combustible material. Thomas *et al.* (2002) have detailed this sequence of events in episodes of oak decline in central Europe. Two primary factors are considered of greatest importance: insect defoliation and either winter frost or summer drought, although infection of foliage by powdery mildew (*Microsphaera alphitoides* Griff. et Maubl.) or the roots by *Phytophthora* spp. can also contribute to the initial stress. Of the secondary causes, wood borers of the genus *Agrilus* have the greatest impact on the health of the tree. Fungi (*Armillaria* spp.) occur on oak roots in the early stage of dying, but appear largely to be saprophytic rather than agents of decline. Considering the long-term impact of exotic pathogens on forest ecosystems, Rackham (2003) suggests that because of the introduction of powdery mildew into Europe in the early 20th century (Thomas *et al.*, 2002), oaks are now less able to regenerate under shade.

Pathogens in the sedimentary record

A number of recent pathogen outbreaks have been examined in the sedimentary record, with such investigations seen as a means of testing the potential for reconstructing biotic disturbances over long time scales using palaeoecological techniques (e.g. Davis, 1981; Allison *et al.*, 1986). The first

Table 1. Stages in forest disturbance events in which fungal diseases and/or insect infestations ('pathogens') are primary or secondary factors; the example of modern oak dieback and their recognition in the sedimentary record.

Stage	Oak dieback	Associated changes in pollen stratigraphy	Other potential sources of sedimentary evidence
Primary stress factor(s)	Summer drought Winter frost Powdery mildew *Phytophthora*	Rapid decline in host/and other vulnerable taxa	*Stress*: tree ring analysis *Causes*: palaeoclimatic data (stable isotopes and from other techniques), pathogens as below
Secondary factors (pathogens)	Bark beetles (*Agrilus*)	Continued low values of host, disturbance indicators, recovery of non-host species	Macrofossils: bark beetles, defoliating insects, leaf damage, fungal bodies, wood remains Spores of parasitic fungi Ancient DNA
Tree death and colonization by saprophytes	*Armillaria* infection	As above	Spores of saprophytic fungi
Abundance of dead wood leading to more frequent fires			Macro/micro-charcoal data
Long-term change in forest composition	Failure of oak to regenerate under shade	Lower long-term abundance of host	
Genetic change in pathogen or host		Recovery in the abundance of host	

such studies were undertaken from the area affected by chestnut blight, which between 1904 and 1950 spread over eastern North America killing 85% of mature *Castanea dentata* ([Marsh] Borkh.) trees (Anderson, 1974). The declines in *Castanea* pollen in lake sediments are sudden, sustained and roughly synchronous over large areas (Anderson, 1974; Davis, 1981). At some sites, increases in tree species associated with chestnut are recorded after the decline, notably *Betula* and *Quercus* (Brugam, 1978). However, attempts to examine the impact of the outbreak on forest composition more widely are hampered by other unrelated land-use changes (Patterson and Backman, 1988). The late 1970s outbreak of Dutch elm disease in southern England has also been subjected to pollen-stratigraphic investigation from a wooded area (Perry and Moore, 1987). A decline in elm pollen is followed by increases in pollen types derived from outside the woodland, indicating changes in pollen dispersal following the disturbance.

More recently, Anderson *et al.* (2010); Morris and Brunelle (2012) and Morris *et al.* (2013) have produced high-resolution stratigraphic records from small sub-alpine lakes in the western USA affected by infestations of the spruce bark beetle (*Dendroctonus rufipennis* Kirby) during the 20th century. Fluctuations in the pollen representation of the host tree (*Picea engelmannii* Parry) and species not affected (notably *Abies lasiocarpa* [Hook.] Nutt) correspond well, in terms of both the timing and the direction of change, with historical records. Morris and Brunelle (2012) and Morris *et al.* (2013) indicate that ratios of host to non-host pollen are a robust method of detecting high-magnitude events. However, changes in the abundance of shrub and herb pollen are short-lived and difficult to detect and expected increases in soil erosion and alterations in nutrient cycling during outbreaks could not be identified in the sedimentary record. Nevertheless, these authors caution that additional lines of evidence (to palynology) are required if Holocene events are to be identified with any certainty.

Two mid-Holocene pollen-stratigraphic events dominate the Quaternary literature on plant pathogens: the hemlock (*Tsuga*) decline in eastern North America and the pan-European elm (*Ulmus*) decline. Both were apparently synchronous across broad geographical regions, with age of the *Tsuga* decline determined at 60 sites to be ca 5 500 cal a BP (Bennett and Fuller, 2002) and the *Ulmus* decline having a mean date of 5 036 ± 247 ^{14}C a BP (ca 5 800 cal a BP) in the British Isles (Parker *et al.*, 2002). Two further unusual features

are associated with these events at many, but by no means all, sites. First, the declines in pollen frequencies are of a large magnitude and rapid, with data from annually laminated sediments suggesting at some sites they occurred over a period of <20 years (Allison *et al.*, 1986; Peglar, 1993). This suggests the death of populations rather than simply the absence of recruitment (Birks, 1986). Secondly, the impact on the pollen representation of *Tsuga* and *Ulmus* is long-lasting which, it has been suggested, indicates the first outbreak of a pathogen (Davis, 1981).

Attributed by Deevey (1939) to climate change, Davis (1981) compared the mid-Holocene hemlock decline with the pollen record of the 20th century *Castanea* decline and, based on the similarities and the features outlined above, concluded that the decline was triggered by the outbreak of a pathogen. Subsequently, finds of the remains of defoliating insects and damaged hemlock needles coincident with the decline (Anderson *et al.*, 1986; Bhiry and Filion, 1996) appeared to corroborate the pathogen hypothesis (Table 2). However, this was not universally accepted as the primary causal process and more recent studies using further lines of evidence, including lake level data, climate modelling and stable isotopes (Hass and McAndrews, 2000; Calcote, 2003; Shuman *et al.*, 2004; Foster *et al.*, 2006; Zhao *et al.*, 2010), strongly suggest the mid-Holocene hemlock decline was triggered by abrupt climate change. Most recently, Oswald and Foster (2012) indicate the event varied geographically and that in some areas a series of droughts produced a stepped decline in *Tsuga* pollen.

The elm decline was initially attributed to climate change, increasing continentality (e.g. Iversen, 1944), then human activity (Troels-Smith, 1960). However, over the last 30 years a broad consensus has emerged that such a widespread and complex event cannot be explained by a single process and that a pathogen is likely to have been a contributory factor (e.g. Birks, 1986; Girling, 1988; Peglar, 1993; Peglar and Birks, 1993; Parker *et al.*, 2002; Rackham, 2003; Clark and Edwards, 2004; Lamb and Thompson, 2005). A number of lines of evidence (Table 2) have been cited in support of an attack by a fungal disease (such as *Ophiostoma*) spread by the elm bark beetle (*Scolytus scolytus* L.). It is argued that the elm decline may be the first example of anthropogenic disturbance facilitating the spread of a pathogen (Lamb and Thompson, 2005). Evidence for such activity is often, but not always, associated with the major reduction in *Ulmus* pollen values and early agriculturists could

Table 2. Evidence offered in support of fungal diseases and/or insect infestations being contributory factors in the mid-Holocene declines of hemlock (*Tsuga*) and elm (*Ulmus*) pollen.

1. The apparent synchronicity of the events across broad geographical regions (see Davis, 1981; Huntley and Birks, 1983; Birks, 1986; Bennett and Fuller, 2002; Parker *et al.*, 2002).

2. The rapidity of the declines in *Tsuga* and *Ulmus* pollen values, as recorded at sites where high-precision dating evidence is available (e.g. Allison *et al.*, 1986; Peglar, 1993; Skog and Regnell, 1995).

3. The long-term impact on the abundance of hemlock and elm. At some sites *Tsuga* does not recover for 2 000 years (Davis, 1981) or in the case of *Ulmus* not at all (Birks, 1986). However, it should be noted that the late Holocene abundance of elm in Europe is likely to have been heavily influenced by human activity (Birks, 1986).

4. Fossil evidence for the contemporaneous presence of phytophagus insects. For the *Tsuga* decline, remains of the hemlock looper (*Lambdina fiscellaria* Gven.) and the spruce budworm (*Choristoneura fumiferana* Clem.), along with hemlock needle damage indicative of hemlock looper feeding, have been found coincident with the decline (Bhiry and Filion, 1996). The elm bark beetle (*Scolytus scolytus* L.) has been recorded before, and from around the time of, the *Ulmus* decline at sites in England, Scotland, Switzerland and Denmark (Girling, 1988; Rasmussen and Christensen, 1997; Clark and Edwards, 2004).

5. Modern outbreaks of virulent strains of fungal pathogens (e.g. chestnut blight, Dutch elm disease) have produced pollen stratigraphic signatures comparable to the mid-Holocene declines (e.g. Brugam, 1978; Davis, 1981; Perry and Moore, 1987).

6. The continued abundance of elm at a site in western Ireland through into the late-Holocene, despite evidence of localized disturbance due to human activity in the mid-Holocene. Lamb and Thompson (2005) suggest that the pathogen, vector or the tree was less susceptible near to the margins of the range of elm.

have been involved directly (by transporting a fungus) or indirectly (e.g. through causing damage favouring infection). Girling (1988) notes that although *S. scolytus* largely attacks dead wood, recently emerged beetles feed on healthy trees which can lead to their infection. Therefore, at some locations, for example where there is no association with human activity, disease might be a primary cause (Rasmussen, 2005). Alternatively, given that the elm decline is often accompanied by reductions in the abundance of other deciduous taxa (e.g. *Tilia*, Grant *et al.*, 2011) and the evidence, from a number of independent sources, for climate variability in Europe during the mid-Holocene (e.g. Langdon *et al.*, 2003; Magny *et al.*, 2006; Olsen *et al.*, 2010; Kühl and Moschen, 2012), the primary stress factor could have been climate change.

Recently obtained evidence relating to pathogen outbreaks during the Holocene include the investigations of Jasinski and Payette (2007) from sites in Québec. These authors have demonstrated the presence back to ca 8 000 cal a BP of the spruce budworm (*Choristoneura fumiferana* Clem.) and the fungus *Lophodermium piceae* ([Fckl.] Hoehn.), which is associated with the needles of *Picea mariana* (Mill.). It is suggested that the co-occurrence of the budworm remains and fungal fruiting bodies indicate that spruce budworm infestations resulted in an increase in fungal infection and/or fructification, although drought is acknowledged as an alternative stress factor. In addition, remains of the spruce bark beetle *Dendroctonus* spp. have been reported from two lakes in the northern Rocky Mountains, USA (Brunelle *et al.*, 2008). The evidence is compatible with infestations occurring ca 8 200 cal a BP, during a short-lived period of cooler and wetter conditions (e.g. Alley *et al.*, 1997; Daley *et al.*, 2011). This is consistent with the findings of Sherriff *et al.* (2011) who, using tree ring data for the period 1600–2007, showed that outbreaks of *Dendroctonus rufipennis* in southern Alaska were related to climate variability and, over multi-decadal time scales, preceded by cool-phase Pacific Decadal Oscillation conditions.

Finally, fungal spores are increasingly being recorded alongside pollen in sedimentary records. High values of *Kretzschmaria deusta* ([Hoffm] P.M.D. Martin), a mild parasite of deciduous trees, have been reported from a number of sites. They occur after trees are likely to have been subject to stress from flooding (Kuhry, 1985; Waller and Grant, 2012) or human activity (van der Wiel, 1982) and have notably been recorded at a site in north Wales after the elm decline (Innes *et al.*, 2006). In addition, Latałowa *et al.* (2013) report the sustained abundance of *K. deusta* spores over the interval ca 8 000–5 300 cal a BP from a mire in northern Poland and suggest that the perpetual activity of this fungus may have influenced vegetation composition. High frequencies of *Tilia* pollen (and therefore warm summers) and coprophilous fungal spores are also recorded during this period, with drier conditions and animal damage likely to have contributed to the infection of *Tilia* by *K. deusta*. The ability of *Tilia* to respond to these attacks by the vegetative production of basal sprouts could not only have enabled the long-term survival, but also promoted the local dominance, of *Tilia* (Latałowa *et al.*, 2013).

Towards a better understanding of the long-term history of disturbance events

The investigations undertaken to date suggest that palaeoecology can contribute to a better understanding of forest disturbance episodes involving pathogens, both large-scale and gap-phase events. However, this potential has yet to be fully realized. Pathogen-focused research strategies, informed by an understanding of the interactions and chain of events within which pathogens are active, are required. In conjunction with multi-site pollen investigations undertaken at an appropriate temporal resolution, additional complementary evidence needs to be collected (Table 1).

Wood remains have considerable potential. Tree ring analysis offers a direct means of demonstrating stress. For example, Bhiry and Filion (1996) report decreases in radial growth associated with recent hemlock lopper outbreaks in Québec and in fossil *Tsuga* remains dating back to ca 5 650 cal a BP. Periods of accelerated growth due to the death of mature trees and release from competition have also been identified after recent and historical spruce bark beetle outbreaks in Colorado and Alaska (Veblen *et al.*, 1994; Sherriff *et al.*, 2011). Wood remains may also record the pattern of damage caused by bark beetles and fungal attack. For example, Creber and Ash (1990), on the basis of well-defined pockets of decay, were able to attribute damage on Upper Triassic trees in the south-western USA to a pathogenic pocket rot fungus rather than a saprophyte.

Due to the growth in the use of non-pollen palynomorphs for palaeoenvironmental reconstruction and advances in fungal spore identification (e.g. van Geel, 1978, 2001; van Geel and Aptroot, 2006), as previously noted, fungi are increasingly being recorded in association with forest disturbance events. A number of taphonomic issues need to be considered. Fossil records will clearly be biased towards fungi aerially transmitting robust and distinct spores with diseases transmitted by insect-vectors likely to go unrecorded. The spores of *Ophiostoma* are, for example, fragile and unlikely to withstand the procedures used to prepare fossil pollen and spores (Groenman-van Waateringe, 1983). In addition, van Geel and Andersen (1988) have demonstrated that the frequency of *K. deusta* spores, which are produced close to the ground, is influenced by the distance between sampled sites and infected trees and Waller (2010) presents evidence indicating that fungal spore representation can be strongly influenced by changes in depositional environment. It should also be noted that the distinction between pathogens and saprophytes in fungi can be problematic. As noted earlier for *Armillaria*, many fungi, while they may act as parasites, continue to, or mainly, exploit dead hosts.

For the elm decline, particular caution needs to be taken over inferring the presence of a fungal disease from finds of the elm bark beetle (Table 2). Not only are the beetle remains often weakly or not associated with the decline in pollen values, but with the beetle present earlier in the Holocene, fossil occurrence may simply indicate the presence of suitable habitat (Robinson, 2000).

Whether climate change acted as a primary causal agent of a disturbance episode is a testable hypothesis if independent palaeoclimatic data can be obtained (cf. Zhao *et al.*, 2010). Comparison of high-resolution pollen and stable isotope data could, for example, confirm or refute a climatic trigger for the elm decline.

Pathogen attacks are likely to result in an increase in combustible material and therefore to be associated with fires, a connection which can be examined through investigations of charcoal content. Jasinski and Payette (2007) found *L. piceae* remains, along with spruce budworm head capsules, before fire events. In addition, in a well-resolved sequence from Brede Bridge in southern England (Grant and Waller, 2010), a peak in micro-charcoal frequencies occurs approximately 100 years after the start of the elm decline. Such a figure is consistent with an event involving the protracted decline and death of trees.

The importance of pathogens in the past

From the evidence currently available it could be concluded (cf. Davis, 1981) that large-scale pathogen outbreaks were much more infrequent in the past which, given the role that human activity currently plays in transporting pathogens to new locations, would not be surprising. Multi-site, high-resolution, multi-proxy palaeoecological investigations require considerable resources. Can such studies into past pathogen outbreaks be justified? Causal connections between biological trends and climate change are often difficult to establish from short-term studies, and palaeoecology has a role to play in demonstrating the degree to which climate change and pathogen attacks are coupled. The evidence currently available certainly hints at a link with abrupt climate change, although associations between the various proxies are often weak.

Pathogens, even if demonstrated to have been active during disturbance events in the past, could be regarded as simply being secondary factors and their appearance the inevitable consequence of the presence of stressed trees. However, even if not the primary stress factor, pathogens may still have significantly influenced vegetation composition. One of the characteristics of the hemlock and elm declines is that the reductions in the abundance of *Tsuga* and *Ulmus* pollen are long-lived (Table 2). In contrast, associated taxa often decline simultaneously but then recover. Given that pathogens tend to be species specific, by contributing to tree death and the failure of *Tsuga* and *Ulmus* to regenerate, they may in some areas have been the critical factor in causing their hosts to disappear. Host trees in less stressed positions would be vulnerable because of the increased loading of pathogens, with re-infection preventing re-establishment through vegetative means or propagules. Recovery would then have been delayed until resistant stock could reinvade from distance or the virulence of the pathogen was reduced (Table 1). Multi-proximity studies have the potential to address this issue; is the long-term impact of climate change on vegetation composition greater when accompanied by a secondary pathogen attack?

In part, the hemlock and elm declines stand out because of their geographical scale. However as Birks (1986) points out, Holocene pollen records from Europe and North America document many other smaller-scale (regional and local) reductions in the abundance (or extinctions) of tree taxa. Given the role played by non-exotic, as well as introduced, pathogens in influencing the modern distribution of species (Castello *et al.*, 1995; Holdenrieder *et al.*, 2004), multi-proxy investigations are likely to demonstrate that pathogens were an important factor in at least some past changes in forest composition and ultimately to contribute to a better understanding of such episodes. Such knowledge is clearly important as, whether driven directly by human activity or by climate change, ash dieback seems destined to be but one of an increasing number of high-impact pathogen outbreaks.

References

Alley RB, Mayewski PA, Sowers T, *et al.* 1997. Holocene climatic instability: A prominent, widespread event 8200 years ago. *Geology* **25**: 483–486.

Allison TD, Moeller RE, Davis MB. 1986. Pollen in laminated sediments provides evidence for a mid-Holocene forest pathogen outbreak. *Ecology* **6**: 1101–1105.

Anderson PK, Cunningham AA, Patel NG, *et al.* 2004. Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. *Trends in Ecology and Evolution* **19**: 535–544.

Anderson RS, Davis RB, Miller NG, *et al.* 1986. History of late- and post-glacial vegetation and disturbance around Upper South Branch Pond, northern Maine. *Canadian Journal of Botany* **64**: 1977–1986.

Anderson RS, Smith SJ, Lynch AW, *et al.* 2010. The pollen record of a 20th century spruce beetle (*Dendroctonus rufipennis*) outbreak in a Colorado subalpine forest, USA. *Forest Ecology and Management* **260**: 448–455.

Anderson TW. 1974. The chestnut pollen decline as a time horizon in lake sediments in eastern North America. *Canadian Journal of Earth Sciences* **11**: 678–685.

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

Bhiry N, Filion L. 1996. Mid-Holocene hemlock decline in eastern North America linked with phytophagous insect activity. *Quaternary Research* **45**: 312–320.

Birks HJB. 1986. Late-Quaternary biotic changes in terrestrial and lacustrine environments, with particular reference to north-west Europe. In *Handbook of Holocene Palaeoecology and Palaeohydrology*, Berglund BE (ed.). Wiley: Chichester; 3–65.

Brasier CM. 2001. Rapid evolution of plant pathogens via interspecific hybridization. *Bioscience* **51**: 123–133.

Brasier CM, Buck KW. 2002. Rapid evolutionary changes in a globally invading fungal pathogen (Dutch elm disease). *Biological Invasions* **3**: 223–233.

Brasier CM, Kirk SA, Delcan J, *et al.* 2004. *Phytophthora alni* sp. nov. and its variants: designation of emerging heteroploid hybrid pathogens spreading on *Alnus* trees. *Mycological Research* **108**: 1 172–1 184.

Brugam RB. 1978. Pollen indicators of land-use change in southern Connecticut. *Quaternary Research* **9**: 349–362.

Brunelle A, Rehfeldt GE, Bentz B, *et al.* 2008. Holocene records of *Dendroctonus* bark beetles in high elevation pine forests of Idaho and Montana, USA. *Forest Ecology and Management* **255**: 836–846.

Calcote R. 2003. Mid-Holocene climate and the hemlock decline: the range limit of *Tsuga canadensis* in the western Great Lakes region, USA. *The Holocene* **13**: 215–224.

Castello JD, Leopold DJ, Smallidge PJ. 1995. Pathogens, patterns, and processes in forest ecosystems. *Bioscience* **45**: 16–24.

Clark SHE, Edwards KJ. 2004. Elm bark beetle in Holocene peat deposits and the northwest European elm decline. *Journal of Quaternary Science* **19**: 525–528.

Creber GT, Ash SR. 1990. Evidence of widespread fungal attack on Upper Triassic trees in the southwestern USA. *Review of Palaeobotany and Palynology* **63**: 189–195.

Daley TJ, Thomas ER, Holmes JA, *et al.* 2011. The 8200 yr BP cold event in stable isotope records from the North Atlantic region. *Global and Planetary Change* **79**: 288–302.

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.

Deevey ES Jr. 1939. Studies on Connecticut lake sediments. I. A postglacial climatic chronology for southern New England. *American Journal of Science* **237**: 691–724.

Desprez-Loustau ML, Robin C, Buée M, *et al.* 2007. The fungal dimension of biological invasions. *Trends in Ecology and Evolution* **22**: 472–480.

Dwyer G, Dushoff J, Yee SH. 2004. The combined effects of pathogens and predators on insect outbreaks. *Nature* **430**: 341–345.

Foster DR, Oswald WW, Faison EK, *et al.* 2006. A climatic driver for abrupt mid-Holocene vegetation dynamics and the hemlock decline in New England. *Ecology* **87**: 2959–2966.

Gadgil PD. 1977. Duration of leaf wetness periods and infection of *Pinus radiata* by *Dothistroma pini*. *New Zealand Journal of Forest Science* **7**: 83–90.

Gil L, Fuentes-Utrilla P, Soto A, *et al*. 2004. Phylogeography: English elm is a 2,000-year-old Roman clone. *Nature* **431**: 1053.

Girling MA. 1988. The bark beetle *Scolytus scolytus* (Fabricius) and the possible role of elm disease in the early Neolithic. In *Archaeology and the Flora of the British Isles*, Jones M (ed.). Oxford University Committee for Archaeology: Oxford; 34–38.

Grant MJ, Waller MP. 2010. Holocene fire histories from the edge of Romney Marsh. In: *Romney Marsh: Persistence and Change in a Coastal Lowland*, Waller MP, Edwards E, Barber L (eds). Romney Marsh Research Trust: Sevenoaks; 53–73.

Grant MJ, Waller MP, Groves JH. 2011. The *Tilia* decline: vegetation change in lowland Britain during the mid and late Holocene. *Quaternary Science Reviews* **30**: 394–408.

Groenman-van Waateringe W. 1983. The early agricultural utilization of the Irish landscape: the last word on the elm decline. In *Landscape Archaeology in Ireland*, Reeves-Smyth T, Hammond F (eds.) British Archaeological Reports, British series 1st Vol. 16, Oxford; 217–232.

Haas JN, McAndrews JH. 2000. The summer drought related hemlock (*Tsuga canadensis*) decline in Eastern North America 5700 to 5100 years ago. In *Proceedings: Symposium on Sustainable Manangement of Hemlock Ecosystems in Eastern North America (Durham, New Hampshire, USA, 1999)*, McManus K, Shields KS, Souto DR (eds). USDA Forest Service General Technical Report NE-267; 81–88.

Holdenrieder O, Pautasso M, Weisberg PJ, *et al*. 2004. Tree diseases and landscape pathology: the challenge of landscape pathology. *Trends in Ecology and Evolution* **19**: 446–452.

Huntley B, Birks HJB. 1983. *An Atlas of Past and Present Pollen Maps for Europe: 0–13000 Years Ago*. Cambridge University Press: Cambridge.

Husson C, Scala B, Caël O, *et al*. 2011. *Chalara fraxinea* is an invasive pathogen in France. *European Journal of Plant Pathology* **130**: 311–324.

Innes JB, Blackford JJ, Chambers FM. 2006. *Kretzschmaria deusta* and the North West European mid-Holocene *Ulmus* decline at Moel y Gerddi, North Wales, United Kingdom. *Palynology* **30**: 121–132.

Iversen J. 1944. *Viscum, Hedera* and *Ilex* as climatic indicators. *Geologiske Föreningens Stockholm Förhandlingar* **66**: 463–483.

Jasinski JP, Payette S. 2007. Holocene occurrence of *Lophodermium piceae*, a black spruce needle endophyte and possible paleoindicator of boreal forest health. *Quaternary Research* **67**: 50–56.

Jung T, Blaschke H, Oswald W. 2000. Involvement of soilborne *Phytophthora* species in central European oak decline and the effect of site factors on the disease. *Plant Pathology* **49**: 706–718.

Kraj W, Zarek M, Kowalski T. 2012. Genetic variability of *Chalara fraxinea*, dieback cause of European ash (*Fraxinus excelsior* L.). *Mycological Progress* **11**: 37–45.

Kühl N, Moschen R. 2012. A combined pollen and δ^{18}O *Sphagnum* record of mid-Holocene climate variability from Dürres Maar (Eifel, Germany). *The Holocene* **22**: 1075–1085.

Kuhry P. 1985. Transgression of a raised bog across a coversand ridge originally covered with an oak–lime forest. *Review of Palaeobotany and Palynology* **44**: 303–353.

Lamb H, Thompson A. 2005. Unusual mid-Holocene abundance of *Ulmus* in western Ireland – human impact in the absence of a pathogen? *The Holocene* **15**: 447–452.

Langdon PG, Barber KE, Hughes PDM. 2003. A 7500-year peat-based palaeoclimatic reconstruction and evidence for an 1100-year cyclicity in bog surface wetness from Temple Hill Moss, Pentland Hills, southeast Scotland. *Quaternary Science Reviews* **22**: 259–274.

Latałowa M, Pedziszewska A, Maciejewska E, *et al*. 2013. *Tilia* forest dynamics, *Kretzschmaria deusta* attack, and mire hydrology as palaeoecological proxies for mid-Holocene climate reconstruction in the Kashubian Lake District (N Poland). *The Holocene*. DOI: 10.1177/0959683612467484

Liebhold AM, Haynes KJ, Bjørnstad ON. 2012. Spatial synchrony of insect outbreaks. In *Insect Outbreaks Revisited*, Barbosa P, Letourneau DK, Agrawal AA (eds). Wiley: Chichester; pp. 113–125.

Magny M, Leuzinger U, Bortenschlager S, *et al*. 2006. Tripartite climate reversal in central Europe 5600–5300 years ago. *Quaternary Research* **65**: 3–19.

Morris JL, Brunelle A. 2012. Pollen accumulation in lake sediments during historic spruce beetle disturbances in subalpine forests of southern Utah, USA. *The Holocene* **22**: 961–974.

Morris JL, le Roux PC, Macharia AN, *et al*. 2013. Organic, elemental, and geochemical contributions to lake sediment deposits during severe spruce bark beetle (*Dendroctonus rufipennis*) disturbances. *Forest Ecology and Management* **289**: 78–89.

Olsen J, Noe-Nygaard N, Wolfe BB. 2010. Mid-to late-Holocene climate variability and anthropogenic impacts: multi-proxy evidence from Lake Bliden, Denmark. *Journal of Paleolimnology* **43**: 323–343.

Oswald WW, Foster DR. 2012. Middle-Holocene dynamics of *Tsuga canadensis* (eastern hemlock) in northern New England, USA. *The Holocene* **22**: 71–78.

Parker AG, Goudie AS, Anderson DE, *et al*. 2002. A review of the mid-Holocene elm decline in the British Isles. *Progress in Physical Geography* **26**: 1–45.

Patterson WA III, Backman AE. 1988. Fire and disease history of forests. In *Vegetation History*, Huntley B, Webb T III (eds). Kluwer Publishers: Dordrecht; 603–632.

Pautasso M, Aas G, Queloz V, *et al*. 2013. European ash (*Fraxinus excelsior*) dieback-A conservation biology challenge. *Biological Conservation* **158**: 37–49.

Peglar SM. 1993. The mid-Holocene *Ulmus* decline at Diss Mere, Norfolk, UK: a year-by-year pollen stratigraphy from annual laminations. *The Holocene* **3**: 1–13.

Peglar SM, Birks HJB. 1993. The mid-Holocene *Ulmus* fall at Diss Mere, south-east England – disease and human impact? *Vegetation History and Archaeobotany* **2**: 61–68.

Perry I, Moore PD. 1987. Dutch elm disease as an analogue of Neolithic elm decline. *Nature* **326**: 72–73.

Pimentel D, McNair S, Janecka J, *et al*. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environment* **84**: 1–20.

Pridnya MV, Cherpakov VV, Paillet FL. 1996. Ecology and pathology of European chestnut (*Castanea sativa*) in the deciduous forests of the Caucasus Mountains in southern Russia. *Bulletin of the Torrey Botanical Club* **123**: 223–239.

Rackham O. 2003. *Ancient Woodland: Its History, Vegetation and Uses in England*, 2nd edn. Castlepoint Press: Dalbeattie.

Rasmussen P. 2005. Mid-to late-Holocene land-use change and lake development at Dallund Sø, Denmark: vegetation and land-use history inferred from pollen data. *The Holocene* **15**: 1116–1129.

Rasmussen P, Christensen K. 1997. The mid-Holocene *Ulmus* decline: a new way to evaluate the pathogen hypothesis. www.geus.dk/departments/environ-hist-climate/posters/rasmussen97-dk.htm [accessed 31 December 2012].

Robinson M. 2000. Coleopteran evidence for the elm decline, Neolithic activity in woodland, clearance and the use of the landscape. In *Plants in Neolithic Britain and Beyond*, Fairburn AS (ed.). Neolithic Studies Group Seminar. Papers 5 Oxbow Books: Oxford; 27–36.

Schlarbaum SE, Hebard F, Spaine PC, *et al*. 1997. Three American tragedies: chestnut blight, butternut canker and Dutch elm disease. In *Proceedings, Exotic Pests of Eastern Forests*, Britton KO (ed.). Tennessee Exotic Pests Plant Council, 45–54. www.srs.fs.usda.gov/pubs/ja/ja_schlarbaum002.htm. [accessed 15 February 2013].

Sherriff RL, Berg EE, Miller AE. 2011. Climate variability and spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska. *Ecology* **92**: 1459–1470.

Shuman B, Newby P, Huang YS, *et al*. 2004. Evidence for the close climatic control of New England vegetation history. *Ecology* **85**: 1297–1310.

Skog G, Regnell J. 1995. Precision calendar-year dating of the elm decline in a *Sphagnum*-peat bog in southern Sweden. *Radiocarbon* **37**: 197–202.

Sutherland ML, Pearson S, Brasier CM. 1997. The influence of temperature and light on defoliation levels of elm by Dutch elm disease. *Phytopathology* **87**: 576–581.

Thomas FM, Blank R, Hartmann G. 2002. Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. *Forest Pathology* **32**: 277–307.

Timmermann V, Børja I, Hietala AM, *et al.* 2011. Ash dieback: pathogen spread and diurnal patterns of ascospore dispersal, with special emphasis on Norway. *Bulletin OEPP/EPPO Bulletin* **41**: 14–20.

Troels-Smith J. 1960. Ivy, mistletoe and elm: climatic indicators – fodder plants: a contribution to the interpretation of the pollen zone border VII–VIII. *Danmarks Geologiske Undersøgelse II*, Series IV: **4**: 1–32.

van der Wiel AM. 1982. A palaeoecological study of a section from the foot of the Hazendonk (Zuid-Holland, The Netherlands), based on the analysis of pollen, spores and macroscopic plant remains. *Review of Palaeobotany and Palynology* **38**: 35–90.

van Geel B. 1978. A palaeoecological study of Holocene peat bog sections in Germany and the Netherlands. *Review of Palaeobotany and Palynology* **25**: 1–120.

van Geel B. 2001. Non-pollen palynomorphs. In *Tracking Environmental Change Using Lake sediments Vol. 3: Terrestrial, Algal and siliceous Indicators*, Smol JP, Birks HJB, Last WM (eds.) Kluwer Publishers: Dordrecht; 99–119.

van Geel B, Andersen ST. 1988. Fossil ascospores of the parasitic fungus *Ustulina deusta* in Eemian deposits in Denmark. *Review of Palaeobotany and Palynology* **56**: 89–93.

van Geel B, Aptroot A. 2006. Fossil ascomycetes in Quaternary deposits. *Nova Hedwigia* **82**: 313–329.

van Opstal NA. 2011. Introduction to the EPPO Workshop on *Chalara fraxinea*, a major threat for ash trees in Europe. *Bulletin OEPP/EPPO Bulletin* **41**: 1–2.

Veblen TT, Hadley KS, Nel EM, *et al.* 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *Journal of Ecology* **82**: 125–135.

Waller MP. 2010. Ashtead Common, the evolution of a cultural landscape. A spatially precise vegetation record for the last 2000 years from south-east England. *The Holocene* **20**: 733–746.

Waller MP, Grant MJ. 2012. Holocene pollen assemblages from coastal wetlands: differentiating natural and anthropogenic causes of change in the Thames estuary, UK. *Journal of Quaternary Science* **27**: 461–474.

Wood DM, Parry D, Yanai RD, *et al.* 2010. Forest fragmentation and duration of forest tent caterpillar (*Malacosoma disstria* Hubner) outbreaks in northern hardwood forests. *Forest Ecology and Management* **260**: 1193–1197.

Woods A, Coates DK, Hamann A. 2005. Is an unprecedented *Dothistroma* needle blight epidemic related to climate change? *BioScience* **55**: 761–769.

Zhao Y, Zicheng Yu Z, Zhao C. 2010. Hemlock (*Tsuga canadensis*) declines at 9800 and 5300 cal. yr BP caused by Holocene climatic shifts in northeastern North America. *The Holocene* **20**: 877–886.