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FUNGAL MICROBIOLOGY

Forest Health in a Changing World

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Abstract Forest pathology, the science of forest health and tree diseases, is operating in a rapidly developing environment. Most importantly, global trade and climate change are increasing the threat to forest ecosystems posed by new diseases. Various studies relevant to forest pathology in a changing world are accumulating, thus making it necessary to provide an update of recent literature. In this contribution, we summarize research at the interface between forest pathology and landscape ecology, biogeography, global change science and research on tree endophytes. Regional outbreaks of tree diseases are requiring interdisciplinary collaboration, e.g. between forest pathologists and landscape ecologists. When tree pathogens are widely distributed, the factors determining their broad-scale distribution can be studied using a biogeographic approach. Global change, the combination of climate and land use change, increased pollution, trade and urbanization, as well as invasive species, will influence the effects of forest disturbances such as wildfires, droughts, storms, diseases and insect outbreaks, thus affecting the health and resilience of forest ecosystems worldwide. Tree endophytes can contribute to biological control of infectious diseases, enhance tolerance to environmental stress or behave as opportunistic weak pathogens potentially competing with more harmful ones. New molecular techniques are available for studying the complete tree endobiome under the influence of global change stressors from the landscape to the intercontinental level. Given that exotic tree diseases have both ecologic and economic consequences, we call for increased interdisciplinary collaboration in the coming decades between forest pathologists and researchers studying endophytes with tree geneticists, evolutionary and landscape ecologists, biogeographers, conservation biologists and global change scientists and outline interdisciplinary research gaps.

Keywords Ash dieback · Biodiversity · Epidemiology · Forest resilience · Fungal pathogens · *Hymenoscyphus fraxineus* · Microbes · *Phytophthora ramorum* · Plant pathology · Tree diseases

Introduction

Traditionally, forest pathologists have investigated the symptoms and causes of tree diseases, as well as the methods to prevent them or reduce their damage. In the last decades, there has been a shift in the perspective of forest pathologists because of the recognition that tree diseases play an important ecological role in the overall functioning of forest ecosystems and their health [1, 2]. For example, it is now recognized that native fungal diseases of trees contribute in maintaining the tree species diversity of forests, thereby making them more resilient to other disturbances [3, 4]. Moreover, both native and exotic tree diseases can be regarded as biological control tools which diversify uniform plantations of exotic trees, thereby reducing their commercial value but increasing their biodiversity and aesthetics [5, 6]. However, some invasive exotic pathogens can drive tree species close to extinction [7, 8] and threaten whole ecosystems [9, 10].

Forest pathology is operating in a changing context [11, 12]. Forests are changing due to ecological succession, shifts in species distributions, habitat fragmentation, overexploitation,

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degradation and, in some cases, lack of management. Stakeholder views on forests are also developing, from a traditional focus on the sustainability of timber production to a recognition of the multi-purpose role of many forests, including recreation and the maintenance of clean air and water [13, 14]. At the same time, forest health is challenged worldwide by increased long-distance trade in plant commodities and a rapidly shifting climate [15, 16]. Together, these two global change drivers are likely to increase the opportunities for the establishment, spread and impact of new pests and pathogens.

Researchers interested in forest health are also changing. Taxonomic and morphological expertise is being lost because of the retirement, often without replacement, of many teachers and practitioners [17, 18]. At the same time, modelling is becoming more and more fashionable, also regarding disturbances in forest ecosystems [19, 20]. New molecular methods are being introduced at an accelerating pace, thus making it possible, e.g. to distinguish cryptic species that could previously not be differentiated. Such rapid methodological developments are also a challenge for keeping updated and teaching [21, 22]. In addition, interdisciplinary opportunities are shaping forest pathology in a changing world. For example, the application of landscape ecology tools and perspectives to forest pathology is improving our understanding of regional outbreaks of exotic tree fungal pathogens [23, 24]. New insights on the health of trees have been obtained by investigating the diversity of endophytes of tree species [25, 26]. Interdisciplinary research has also been achieved on the conservation biology implications of exotic tree diseases [27–30].

Various literature reviews are available on these topics, but the subject is developing rapidly so that there is a need for an update focusing on recent studies involving infectious diseases. The main aim of this contribution is, thus, to selectively survey the literature relevant to forest health in a changing world from the last 10 years (but citing previous papers when appropriate). For summaries of previous relevant literature, the reader is referred to other literature reviews (Table 1). A secondary aim of this brief overview is to map some bridges between forest pathology and neighbouring disciplines, from landscape ecology to disease biogeography, global change ecology and research on endophytes. However, these are not the only disciplines at the borders of forest pathology. Due to space constraints, we have for example not covered the literature on (i) environmental pollution and forest health, (ii) tools and indicators for monitoring forest health, (iii) resistance breeding and (iv) defining forest health.

Landscape Pathology

Tree pathogens propagate in heterogeneous landscapes resulting in non-random spatial patterns of disease expression [23]. Using landscape ecology tools and approaches, it is possible to gain a better grasp of the factors associated with variation in tree disease incidence at various sites, e.g. altitude, soil type, slope exposure, stand age and management factors [31–34]. For example, even at the extreme climatic conditions of the treeline environment, topography and moisture-related variables were shown to influence the landscape pattern of white pine (*Pinus albicaulis*) blister rust incidence, due to

Table 1 A selection of literature reviews of the last years (2003–2013) relevant to forest pathology in a changing world. Additional reviews are cited in the text and in each of the listed reviews

Topic	Reference
Evolution of concepts in forest pathology	[255]
Tree diseases and landscape processes	[23]
Phytophthora ramorum: integrative research and management	[256]
Molecular epidemiology of forest pathogens	[257]
Interactive effects of drought and tree pathogens	[258]
The fungal dimension of biological invasions	[259]
Modelling disease spread and control in complex networks	[260]
Forest structure and fungal endophytes	[188]
Forest tree endophytes: are they mutualists?	[25]
UK biosecurity and plant trade	[107]
Exotic *Phytophthora* species as agents of forest change	[252]
Forest pathogens and climate change	[261]
Wood-decaying fungi: conservation and management	[262]
Ancient woodlands: modern threats	[263]
Ecological impacts of exotic forest pathogens	[264]
Fungi and diseases as natural components of healthy forests	[265]
Structural change in the horticultural industry	[141]
Evolution of the international regulation of plant pests	[266]
Climate change and urban tree pests and diseases	[153]
Diversity of dark-septate endophytes	[267]
Networks in plant epidemiology	[142]
Emerging tree diseases in Europe and responses in society	[268]
Climate change and forest diseases	[269]
Diversity of fungal endophytes in temperate forest trees	[189]
Concepts of plant health	[270]
Emergence of the sudden oak death pathogen *Phytophthora ramorum*	[143]
Contributions of genomics to forest pathology	[21]
Phytophthora species in natural ecosystems	[271]
Forests under climate change and air pollution	[128]
Landscape epidemiology of plant diseases	[33]
Interdisciplinary research on *Phytophthora ramorum*	[148]
Biology, epidemiology and control of *Heterobasidion* species	[90]
Biogeography of invasive forest pathogens in Europe	[108]
Forest pathogens as agents of past vegetation change	[272]
Fungal pathogens and drought-induced tree mortality	[273]

Cronartium ribicola [35]. The disease was reported to affect trees in tree islands more than isolated trees.

For generalist plant pathogens, it is important to study their epidemiology not only in the major host of interest, but also in supposedly minor hosts, because these secondary hosts might have a minor economic role, but their co-occurrence can affect the connectivity patterns from the point of view of the pathogen [36, 37]. For example, until the outbreaks in Japanese larch (*Larix kaempferi*) plantations in 2009, the epidemic of *Phytophthora ramorum* in Great Britain was largely driven not by the presence of susceptible, yet dead-end host trees such as *Castanea sativa*, *Fagus sylvatica* and *Quercus ilex*, but by the distribution of *Rhododendron ponticum*, an exotic yet widespread shrub in the UK, which enables sporulation of the pathogen [38].

Landscape features are important determinants of tree disease epidemics, e.g. when dispersal preferentially occurs along streams [39–41] or in combination with the trade in plants [42–44]. Even in soil, tree fungal pathogens can disperse by mycelial growth over considerable distances [45]. For example, genetic analysis of *Armillaria gallica*, a root rot pathogen, in Massachusetts showed that the average size of the fungal individuals (genets) was 0.13 ha and that basidiospores were able to establish new genets at distances up to 2 km [46]. Even larger genets of *Armillaria* species have been reported, for example in the case of *Armillaria borealis*, *Armillaria cepistipes* and *Armillaria ostoyae* in Swiss subalpine forests, with a range between 0.2 and ~7 ha [47]. However, the time since establishment is also important: in the Golden Gate Park in San Francisco, which was established in 1871 on sandy dunes unlikely to support mycelium before the planting of trees, the largest genotypes of *Armillaria mellea* are now about 300 m in length [48]. A host-free barrier can halt mycelial spread, but long distance dispersal limits the efficacy of such control measures [49–51].

Variation in tree disease expression across landscapes can also be influenced by the distribution of host genetic variation [52, 53]. Within European ash (*Fraxinus excelsior*) tree populations, individual differences in susceptibility to ash dieback, due to *Hymenoscyphus fraxineus* [54–56], have been reported from Denmark, Germany, Lithuania, Poland and Sweden, thus providing a sign of hope for the future of ash trees and their associated biodiversity [57–64]. Whilst differences in disease resistance or tolerance among tree provenances have long been recognized [65–67], their implications for the outbreaks of tree pests and diseases across landscapes of seminatural forests (rather than tree plantations) have only recently started to be explored [68–71]. A variety of new genomic tools is available to tackle this and other related issues (Table 2).

Often, site biophysical features mask the effect of landscape variation in tree genetic diversity on disease incidence and severity, which can be clarified by excluding such confounding factors, e.g. comparing the evidence obtained from common garden experiments and from the field [72–74]. Confounding factors are nevertheless widespread in nature, where they can reinforce each other. A study of the influences of site, forest type, and tree host species on the presence of *Armillaria* species in forests of Massachusetts found that stands of *Tsuga canadensis* are relatively resistant to *Armillaria* species, but become susceptible when also affected by insect defoliation and drought [75]. Interactions between forest disturbances were also documented by a study of the effects of wildfire on *P. ramorum* survival in Californian forests, where the pathogen was more likely to persist when wildfires left unburnt patches of bay laurel (*Umbellularia californica*) [76]. The creation of deadwood by *P. ramorum* in redwood (*Sequoia sempervirens*) forests makes wildfires more severe, thus reducing the usual resilience of this tree species to fires [77].

In some tree pathosystems, the landscape patterns of disease incidence and/or severity are affected by interactions with biotic factors. For example, beech bark disease in North America is associated with the invasive beech scale insect *Cryptococcus fagisuga* which predisposes the trees to attack by *Neonectria* fungi. A large-scale study across eastern North America showed that the dispersal behaviour of the insect makes it unlikely that any trees or stands will be spared by beech bark disease [78]. Most of the regions where American beech (*Fagus grandifolia*) is a dominant stand component are affected by the disease, but these areas cover only 30 % of the overall beech distribution [79]. The explanation of this pattern remains a challenge: it is possible that the percentage of American beech unaffected by beech bark disease is higher in northern compared to southern areas of the maritime provinces of New Brunswick, Nova Scotia and Prince Edward Island (Eastern Canada) because the disease arrived later in the north. Yet, more intensive silviculture (which favoured pioneer tree species and reduced the abundance of beech [80]) and colder winters (which are likely to be lethal to the insect [81]) could also play a role. In Europe, where the insect is endemic, beech bark disease has indeed been shown to be more severe in warmer regions [82].

A biotic factor that can reduce tree disease pressure is parasitism on pathogens. The presence in Europe of hypovirulence in the ascomycete *Cryphonectria parasitica*, the causal agent of chestnut blight, explains the reduced virulence of this introduced tree pathogen in Europe compared to North America [83, 84]. The transmission of the virus depends on the population structure of its host, among other factors [85–87]. Recently, this was also shown for the North American chestnut blight pathosystem, which is characterized by a much higher genetic diversity of *C. parasitica* compared to Europe [88]. An additional biotic factor affecting tree disease pressure is human management of woodlands [89]. It is well known that thinning creates an unnatural supply of freshly cut stumps, thus

Table 2 Selected (molecular) methods for the investigation of forest microbiota. See also the reviews by [21, 257, 274, 275]

Method	Example of application	Reference
Cultivation and identification	Investigation of the spatial and temporal dynamics of fungi inhabiting leaves of common ash (*Fraxinus excelsior*)	[187]
Cloning and sequencing of barcode regions	Comprehensive census of soil fungi of *Picea mariana* forests in interior Alaska, with a fungal:plant species ratio of at least 17:1, and a global estimate of fungal species richness of 6 million species	[276]
High-throughput sequencing of barcode regions	Documentation of a correlation between plant and fungal community structure across western Amazonian rainforests using 454 pyrosequencing	[277]
	Examination of *Phytophtora* communities in chestnut forests using 454 pyrosequencing, combined with traditional techniques	[278]
	Estimation of plant species composition from roots sampled across a chronosequence of deforestation in Amazonia using Illumina metabarcoding	[279]
	Study of the impact on soil bacterial communities of the conversion of tropical forests to oil palm plantations	[280]
	Comparison of the diversity of leaf- and root-associated fungal assemblages along an altitudinal gradient	[281]
Shotgun metagenomics	Investigation of microbiota found in different soil types using shotgun metagenomics and (for bacteria) barcoding	[282]
Meta-transcriptomics	Analysis of the diversity of genes expressed by eukaryotes in forest soils	[283]
Assessment of population structure	Study of soil vs. leaf genotypes of *Phytophthora ramorum* under different weather conditions in California using microsatellite markers	[284]
Whole genome sequencing	Comparison of genomes of four *Phytophthora lateralis* individuals (pathogen of *Chamaecyparis lawsoniana*) and development of SNPs markers to track the dispersal of the fungus through trade pathways in Northern Ireland	[285]
Transcriptome characterization	Study of *Armillaria ostoyae* candidate genes involved in host substrate utilization at the host–pathogen interface	[286]

favouring root rot pathogens such as *Heterobasidion* or *Armillaria* [90]. A study of *Armillaria* species in 150 km^2 of ancient unmanaged forests in the Ukrainian Carpathians documented a relative lack of pathogenic compared to saprotrophic *Armillaria* species, thus supporting the view that the disturbances accompanying forest management can increase the incidence of tree fungal pathogens [91].

Tree Disease Biogeography

Given the increased ease of travel, human beings are now moving themselves, plants and associated organisms over the planet, without much afterthought about the potential long-term consequences of this unprecedented long-distance mobility. Also forest pathologists now have the opportunity to widen their analyses beyond the local and landscape levels, to regions, countries and continents [92–95]. Broad-scale research on tree pathogens was pioneered in the 1970s by forest pathologists investigating Dutch elm disease, both in North America and in Europe [96–98]. A large-scale approach was also inherent in research on the decline affecting forests in Europe (Waldsterben) and North America during the 1980s [99–101]. Nowadays, broad-scale forest pathology is made necessary by the realization of the common health problems shared by exotic tree plantations in several continents [102, 103].

When tree health is investigated over biogeographic scales, forest pathology and biogeography merge into tree disease biogeography, the study of the factors determining the distribution of tree diseases over large geographic scales. For example, an investigation of records of seven *Armillaria* species on conifers in Japan showed their association with the host distribution and, thus, with climate [104]. A reconstruction using nucleotide markers of the invasion history in Europe of the fungal virus *Cryphonectria* hypovirus 1 suggested a role of trade patterns for the spread of hypovirulence (e.g. restrictions in trade between Greece and Turkey; Italy as an important European hub for chestnut cultivation and trade [105]). The host of this hypovirus, *C. parasitica*, has been shown to have been introduced repeatedly to both North America and Europe from two genetic lineages present in the native Asiatic range, thus highlighting the importance of restricting trade in potentially infected commodities also after a pathogen has been introduced, so as to avoid the enhancement of genetic diversity of the fungus. Higher genetic diversity of the pathogen not only reduces the spread of hypovirulence but also increases the adaptive potential of the pathogen [106].

One important factor now shaping the distribution and severity of tree fungal diseases is indeed the long-distance trade of plant commodities [107–109]. For instance, genetic analyses have shown the role of tree nurseries in the dispersal across South Africa of *Fusarium circinatum*, which causes pitch canker, a major disease of exotic pine plantations in many countries [110, 111]. In many cases, there is evidence that tree pathogens are likely to have been introduced to a certain region, because of their low levels of genetic diversity and absence of population structure in the invaded area, e.g. for various *Phytophthora* species [112] and the ash dieback pathogen *H. fraxineus* [113, 114]. Also, the high levels of virulence and spatial expansion of a disease which was previously unrecorded in a region is an indicator of the presence of an exotic invasive pathogen, as documented, e.g. for *H. fraxineus*, which is likely to have been introduced to Europe from East Asia [113, 114]. Often, we still do not know the region of origin of such exotic tree diseases, so that surveys in regions with related hosts and a climate similar to the one of the region of the introduction are needed [115]. Also surveys in tree nurseries, together with data about previous long-distance artificial movement of host trees, are useful for reconstructing the invasion history of exotic tree pathogens.

Tree species migrations have happened also in the past and without human help, for example in response to changes in climate, e.g. through the Beringian Strait at times when Asia and North America were connected due to lower sea levels. The fungal pathogen assemblage of *Populus angustifolia*, a cottonwood species found in western North America, was shown to be similar to the one of *Populus* species in Asia and dissimilar to the one of *Populus trichocarpa*, another western North American species, thus confirming the hypothesis that *P. angustifolia* migrated from Asia to North America [116]. Tree fungal pathogens are interesting not only in their own right: they can also provide evidence to understand the migration history of their host tree species.

Nonetheless, genetic studies of tree fungal pathogens tend not to be carried out together with an analysis of the genetic diversity of their hosts. For example, a genetic study of the root rot pathogen *A. mellea* in the Western and Eastern USA found genetic divergence between the two regions, with Eastern populations likely to have resulted from multiple introductions [117]. Also *Ophiognomonia clavigignenti-juglandacearum*, which has caused range-wide mortality of butternut trees (*Juglans cinerea*) in North America, was shown using genetic analyses to be likely to have been introduced several times, given the geographic clustering of the pathogen genotypes [118]. A single source site in North America and introduction site in central Italy (Castelporziano) was instead inferred for *Heterobasidion irregulare*, a root rot pathogen whose genetic diversity in the Italian invasive range decreases with the distance from its putative introduction site [119]. A country-wide Swiss study of the genetic diversity of *A. cepistipes*, a wood-decaying, native fungus that can also be pathogenic when trees have been stressed by other causes, found no isolation by distance despite a long history of forest fragmentation in the Swiss plateau, with fungal gene flow limited by the Alps only [120].

It is important to study the genetic diversity levels of exotic tree pathogen populations because more genetically diverse pathogens are more likely to overcome resistance [121–123]. Resistance (or tolerance) can be present in some tree individuals despite lack of co-evolution with the pathogen (as for European ash, *F. excelsior*, against ash dieback [64, 113]) or can be obtained after long screening and breeding programmes [124–126]. It is important to preserve the genetic diversity of tree species in such breeding efforts, because this is an insurance against other environmental stresses, pests and diseases.

Global Change and Tree Health

Global change is a process involving the interaction between climate and land use change, increased pollution, trade and urbanization, as well as the invasion of exotic species. All these factors, by modifying the effects of disturbances such as wildfires, droughts, storms, diseases and herbivore outbreaks, are likely to affect the health of forests throughout the planet, although to varying degrees depending on the resilience of each ecosystem [127–129]. Climate shifts over the next decades are expected to lead to novel ecosystems, because of the likely phenological changes and migration of species to cope with the new climatic conditions, together with the artificial long-distance movement of both hosts and pathogens [130–132]. For trees (and their associated organisms), this is likely to lead to selective pressure (in different directions) at the rear, centre and expanding edge of the distribution range [133]. In some cases, tree species are not expected to be able to cope with the rapidity of the climate shifts, so that assisted migration has been suggested to be necessary. This might lead to additional forest health problems in case of unintentional transfer of tree pathogens [134].

Predictions of likely changes in tree disease occurrence and severity under climate change are complicated by model uncertainties in the expected shifts in precipitation, an important factor for the life cycle of many plant pathogens. For example, models of the risk of occurrence of *Phytophthora cinnamomi* in the southwestern USA under likely future climate change scenarios suggest that even if temperature rises are likely to greatly expand the distribution range of the pathogen, reductions in spring precipitation might still constrain that expansion [135]. A further source of uncertainty is the lack of knowledge of the potential effects of climate change and other global change drivers on competitors, mutualists and enemies of tree diseases and insect herbivores [136]. In some cases, for instance when tree disease severity is already high, climate shifts might not result in additional facilitation of fungal infection, as shown by experiments on the effects of high and low precipitation, increased air temperature and *Cytospora chrysosperma* canker infection on *Salix monticola* biomass in Colorado [137]. Many tree host-pathogen interactions currently resulting in disease are dependent on suitable climatic conditions during critical life cycle phases of the pathogen [138]. Climate change might well disrupt such synchronicity, as shown e.g. for the predicted reduction in summer moisture in the 2080s in British Columbia, which would reduce the climate suitability for spore discharge and germination of cedar leaf blight (*Didymascella thujina*) [139].

Climate change will not operate alone, but together with increased quantities of plant commodities traded over long distances, e.g. bonsai and other ornamental plants, nursery stock, seed, wood and wood packing materials [140–142]. For example, the sudden oak death pathogen *P. ramorum* and other *Phytophthora* tree pathogens were widely distributed by the nursery trade in the USA [143–146] and other countries [147–150]. There is also evidence for long-distance dispersal of the ash dieback pathogen by latently infected plants [151] (Fig. 1). This makes it clear that networks spreading information about a certain disease (i.e. the communication channels among researchers, practitioners and other stakeholders) need to be more efficient than networks spreading the disease. However, we have still little knowledge about the structure of plant trade networks compared to animal trade networks and human social networks [109].

Much of the plant trade is directed towards urbanized areas, where most of the retailers and customers are located. Given the heat island effect of urbanization, towns provide a repeated experiment combining climate warming with the introduction of exotic plants and pathogens. It would thus make sense to focus some of the monitoring of new tree health problems in and around towns, because this would often be likely to enable early recognition of new outbreaks [152–154]. To some extent, this is already the case given that urbanized areas tend to have more observers than rural regions [155]. Trees in urban alleys, squares and parks are subjected to many sources of stress other than disease, including (i) high levels of air, water and soil pollution, (ii) wounds due to repeated pruning and (iii) soil compaction and sealing. Chronic stress can debilitate urban trees and facilitate the action of secondary pathogens. In the urban forest of Perth, in southwestern Australia, a diversity of *Phytophthora* species was detected [156], thus confirming the suitability of the urban environment for many tree pathogens. In addition, trees planted in urban parks, gardens and streets often originate from tree nurseries, a hub for the dissemination of the many organisms associated with trees.

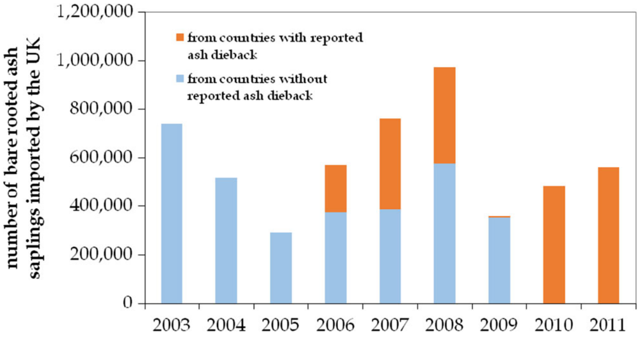


Fig. 1 Number of ash saplings imported between 2003 and 2011 by the UK from EU countries registered on the Forest Reproductive Material database (Belgium, France, Germany, Hungary, Ireland, the Netherlands). Data were obtained from [151]. The *orange colour* indicates ash saplings imported from countries which had already reported the presence of ash dieback. The pathogen was described as a new species by Kowalski in 2006 [54]

Forest pathologists are thus confronted with a changing world, not just because there are now data and tools to study regional outbreaks of tree pathogens over landscape to continental scales, but also because tree health is increasingly challenged by global change drivers and their interactions [157–159]. The increasing number of newly reported tree pathogens over the last decades is a sobering reminder of the tree health problems to come. Indeed, the likely causes of new exotic tree diseases (increased trade, higher temperatures, shifts in host distribution) are supposed to intensify in the next future [160–162]. First reports of crop pests and pathogens have already been reported to have shifted towards the poles, possibly in relation to a warming climate and a stronger increase in economic activities in extratropical countries [163, 164].

Tree Endophytology

In addition to variation in (i) the genetic make-up of hosts, (ii) virulence among pathogen strains and (iii) environmental (including global change) factors, tree health over local to landscape and geographic scales is affected by endophytic assemblages within trees [25, 26, 165, 166]. A beneficial effect of endophytes on tree health has been demonstrated experimentally (reviewed by [26]). Recently, this effect was confirmed for example by studies showing that (i) various leaf endophytes contribute to *Melampsora* rust resistance in poplar [167] and (ii) tree root endophytes can control soil pathogens [168, 169]. Moreover, enhancement of tolerance to abiotic stresses by endophytes has been reported [170–175]. Endophytes can also enhance pathogen virulence—a potentially useful effect for the control of invasive plant species [176]. It is possible that, by systemic induction of defence responses, some leaf endophytes might enable trees to withstand pathogen attacks to other plant organs [177, 178]. Nevertheless, the importance of root endophytes should not be overlooked just because they have tended to be less studied than leaf endophytes [179].

It has been suggested that tree endophytes could be used as indicators of the health and vitality of trees [180, 181]. Tree (fungal) endophytes would be a suitable bio-indicator because they have been shown to be ubiquitous [25, 182]. Moreover, some endophytes can turn from mutualistic or neutral to pathogenic depending on the environmental and host conditions [25, 183, 184]. Tree endophytes could thus be used to track variations in forest health conditions, by taking into account that the factors shaping tree endophytic assemblages vary in space and time, for example the season of the year [185, 186].

However, using endophytes as health indicators is still problematic because endophytic assemblages are shaped by many further factors, including leaf age [187], host physiological status and genetic variation [188–190]. Host genotype is an important determinant of tree endophytes, as shown for example in *Populus balsamifera* growing in a common garden in Fairbanks, Alaska [191]. The right host genotype might be required for successful infection by a particular endophyte genotype, as shown by a study of *Venturia ditricha*, a common foliar endophyte of birch trees [192]. Interestingly, lower frequency and diversity of endophytes have been reported for clones of elms resistant to Dutch elm disease compared to resistant ones [193]. When studied across several dozens of tree species in sub-tropical, cool temperate and sub-boreal forests in Japan, the presence of xylariaceous endophytes was dependent on plant family and leaf traits, thus leading to a certain degree of host recurrence [194].

In addition to host-related traits, variation in tree endophyte assemblages has been shown to be associated with environmental gradients [195, 196]. Relevant factors include the following:

- altitude, e.g. for *F. sylvatica* leaves in the Pyrenees [197];
- latitude, e.g. for *Pinus sylvestris* needles in Finland [198];
- temperature, as found in Japan for *Fagus crenata* [199]
- as well as precipitation, as documented for *Metrosideros polymorpha* in the Hawaii [200].

A further issue is the pervasive (but to varying degrees) presence of human influences on forests, e.g. due to silviculture and gradients in land use intensity [201–204]. Given the many confounding factors, studies of endophyte assemblages in single stands and across landscapes are often not conclusive regarding the causal influence of environmental features on endophytic assemblages, because of the co-variation among explanatory factors (e.g. host distribution and climate [205]) and the lack of experimental controls. It can indeed be difficult to clarify the relative contributions of such factors in shaping tree endophyte diversity, as shown by a study of the influence of host identity and location on endophytes of trees of the Cupressaceae family [206]. A study of leaf endophytic fungi of three *Nothofagus* species growing in four mixed stands in New Zealand found that the diversity of endophytes was more affected by host species than by site [207]. As with tree pathogens, multi-scale studies can help disentangle the factors governing endophyte assemblages at different spatial resolutions [208]. A study of *F. sylvatica* endophytes in a forest stand in southeastern France found that the differences between assemblages of phyllosphere fungi increased with distance between sampled leaves within a single tree canopy and with genetic distance (rather than spatial distance) between sampled trees within the stand [209].

Although the endophytes of only about 10 % of the ~1000 temperate tree species have been investigated so far [189], tree endophytes have tended to be studied in extratropical regions, particularly in North America, Europe and Japan [195, 210]. Given the high diversity of tree species in the tropics and given that endophytic assemblages appear to be specialized to their hosts, it is reasonable to expect that tropical forests harbour a great diversity of endophytic species, which still need to be studied to better understand their role in ecosystem functioning [211]. This goal is a challenge, because of the difficulties inherent in cultivating tree endophytes and their sheer diversity [212]. Determining the fungal endophyte species hosted by trees, particularly in the tropics, is also hampered by the lack of taxonomic knowledge for many fungal genera [213]. But also outside of the tropics, new fungal endophyte species are routinely encountered, as shown by a study of the phyllosphere of *Cephalotaxus harringtonia* in Japan and France [214].

Studying diversity data of fungal endophytes that rely only on cultures in the lab can overlook species that are difficult to culture, that grow slowly or those that are rare [215, 216]. Over the last few years, advances in molecular methods have made it easier to obtain more exhaustive data about the diversity of tree endophytes ([189, 217] and literature listed in Table 2). This trend is expected to continue. There is thus an opportunity to consider tree endophytes in local, landscape and regional studies of tree diseases [218]. It is important to realize that there is often a continuum ranging from pathogenic to neutral and mutualistic status and that we still have little knowledge of the asymptomatic hosts for many pathogens with a cryptic biology [219].

Conclusions

Forest pathologists have to act in a world that is rapidly changing in many respects, from the emergence of new, aggressive exotic tree pathogens to the development of just as new molecular techniques. These developments lead to the increased need for interdisciplinary collaboration, e.g. involving (i) forest pathologists in research on assisted migration of tree species, (ii) the collaboration of geneticists of trees and of tree diseases and (iii) surveys of the network connectivity patterns of tree nurseries and their customers, thus leading to data suitable for analysis by network epidemiologists

[220–222] (Table 3). This overview of recent literature provides evidence that forest pathology is a subject that has established links with various other disciplines.

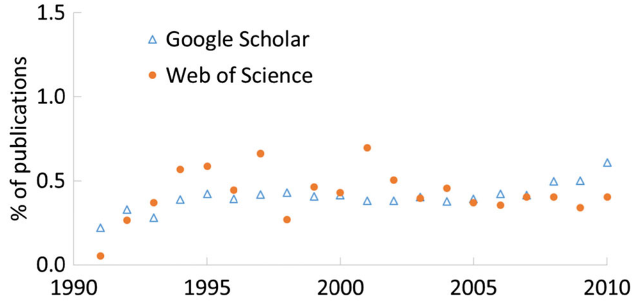
Remarkably, the proportion of publications in forest sciences mentioning ‘forest health’ and ‘tree disease(s)’ has remained stable (at about one out of 200, or ~0.5 % and one out of 2000, or ~0.05 %, respectively) over the 1990s and 2000s (Fig. 2), despite, e.g. methodological developments, the rise of electronic publishing and the emergence of various new exotic tree diseases. However, the absolute numbers of research publications on both forests and forest health/tree diseases have increased steadily over the last two decades. Whether the proportion of interdisciplinary studies related to forest health and tree diseases has remained stable or has increased is a knowledge gap that needs collaboration between forest pathology and scientometrics [223–225]. In this concluding section, we point out some research gaps and opportunities for further research at the interface between forest pathology and neighbouring fields, with particular attention to endophytes (Table 3).

Research on landscape features facilitating the establishment and spread of exotic tree diseases appears to have developed largely independently of research on the factors shaping tree endophyte assemblages, but landscape ecology tools and approaches can be beneficial also in the study of tree endophytes. More diverse landscapes are likely to be less conducive to the spread of exotic tree diseases under changing environmental conditions [226]. This insurance effect of landscape diversity applies in some cases also to insect defoliators, despite their ability to jump from patch to patch of suitable hosts [227]. There is evidence from an archipelago in south-western Finland that birch leaf endophytes are affected to some extent by landscape fragmentation [228], but further studies from other systems are needed to assess whether lack of landscape connectivity generally reduces the protective role of tree endophytes against diseases.

Table 3 A selection of interdisciplinary research gaps relevant to forest health in a changing world

- Forest pathogens and shifting treelines
- Tree diseases in novel ecosystems
- Effects of global change drivers on associated microbiota of tree diseases
- Interacting disturbances and forest health in a changing climate
- Landscape epidemiology of tree pathogens dispersed by trade networks
- Comparative epidemiology of tree diseases in old-growth forests vs. tree monocultures
- Public understanding of the role of tree diseases for the health of forest ecosystems
- Using towns as replicated experiments combining warmer climates, exotic tree hosts and increased propagule pressure of exotic tree pathogens
- Comparing endophytes with other bio-indicators of forest health (e.g. lichens, birds, insects and deadwood)
- Human impacts on large-scale patterns of tree endophytic assemblages
- Forest tree species diversity and tree endophyte biodiversity
- Endophytic assemblages in exotic trees
- Risks for native species associated with plantations of exotic trees
- Mechanisms of endophytic switches from mutualistic or neutral to pathogenic lifestyle
- Evolutionary epidemiology of emerging tree pathogens

(a) Proportion of publications on forests mentioning "forest health" in Google Scholar and Web of Science over the period 1991-2010



(b) Proportion of publications on forests mentioning "tree disease(s)" in Google Scholar and Web of Science over the period 1991-2010

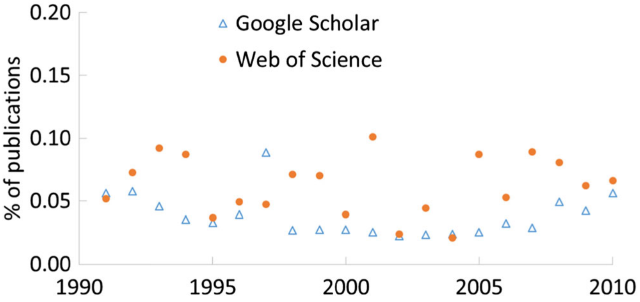


Fig. 2 Temporal trend in the proportion of publications on forests mentioning **a** forest health and **b** tree disease(s) (obtained by dividing the number of papers retrieved each year searching for the keyword ‘forest health’ (or ‘tree disease’) by the number of papers retrieved that year with the keyword ‘forest’), in Google Scholar and Web of Science (1991–2010, as abstracts are searched in Web of Science starting from 1991 only; some papers published after 2010 may still need to be indexed). Data were retrieved in March 2014. Whilst these proportions have remained fairly stable, the absolute number of new yearly publications (both on forests and on forest health/tree diseases) has progressively increased in both databases

Despite the many landscape (and network) metrics that can be calculated in geographic information systems, field data are important also in landscape studies of tree pathogens, as shown by the better performance of models using direct measurements of the density of *P. ramorum* hosts compared to models using remotely sensed estimates of host habitat in California [229]. Predicting tree pathogen and endophyte assemblages from satellite measurements might still look like an outlandish research proposal, but could well take place over the next years. Comparative studies of tree microbial assemblages using remotely sensed data vs. field measurements of habitat variables would be needed to test the viability of this idea.

Regional tree mortality due to more frequent and severe forest disturbances can have ecosystem impacts through changes in plant species composition [230]. Widespread tree mortality can lead to the loss of many associated organisms, as feared for ash dieback over the coming years [29, 231–233]. Our understanding of the biodiversity consequences of exotic tree diseases is still limited to a few pathosystems and groups of organisms [234–237]. Relatively, little information is available on the potential consequences of outbreaks of exotic tree pathogens for their associated microbiota, as most research has focused on the effects on endophytes of endemic tree pathogens [238–245]. A similar lack of knowledge applies to the likely impacts of global change drivers on fungal endophytes.

An important requirement for successfully managing exotic tree diseases such as ash dieback, Sudden Oak Death and Dutch elm disease is collaboration with social scientists and engagement with stakeholders [246–248]. Tree health is just one of the many aims of land management, so that multi-criteria risk analyses are needed to assess the impact of various forest management scenarios on forest ecosystem services [249]. Often, national forest inventories deliver only coarse information for the study of specific tree health problems, thus making tailored surveys necessary for particular diseases [250]. For example, many forest inventories clump together all broadleaved tree species in one category, whereas standardized data on e.g. *F. excelsior* would be needed to assess the potential impacts of ash dieback in various regions.

Exotic tree pathogens have not just environmental and evolutionary consequences [251], but can also be costly economically [252]. Studies of the landscape features associated with tree disease incidence can help prioritize monitoring efforts [253]. A study of limber pine (*Pinus flexilis*) stands at risk of infestation by *C. ribicola* across Wyoming (where pine blister rust has long been present) and Colorado (where it is now becoming established) found that about half of the variation among plots in disease incidence could be explained using environmental variables (e.g. climate data at 1-km resolution) available to land managers [254]. There is the need to adopt similar approaches in the study of regional variations of tree endophyte assemblages.

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