New Phytologist

Forum

Viewpoint

Advancing forest pathology: the need for community-driven molecular experimental model systems

Summary

Forests world-wide are under escalating threat from emerging and invasive fungal and oomycete pathogens, driven by globalization and shifting climate dynamics. Effective strategies to manage the current scale and rate of changes in forest health remain hindered by our limited ability to study the underlying mechanisms of pathogen–host and pathogen–microbiome interactions, especially at a molecular and cellular level, compared to general plant pathology, where experimental and model systems exist. Such models facilitate the integration of diverse methodologies from a broader base of the research community, allowing for a more holistic and deeper examination of complex research questions. Here, we propose a framework for the development of such model systems also for forest pathology. This goal is more feasible than ever, thanks to rapid technological advancements, increasing open data availability and a globally interconnected research community. These factors create a unique opportunity to integrate ecosystem-focused research in forest pathology with a unified model organism strategy. Achieving this goal will require a dedicated community effort in the coming years, as such model systems are not discovered but built.

Integrative approaches are needed to mitigate threats to forest ecosystems

Forests world-wide are under imminent threat due to a complex interplay of direct anthropogenic activities and the repercussions of ongoing climate change (Williams *et al*., 2023). One direct consequence is heightened vulnerability to a range of pathogens, including newly introduced pathogens from globalization, pathogen range expansions in areas where they already occur and latent pathogens within the microbiome whose activity is induced by changes in host–plant interactions (Boyd *et al*., 2013; Brader *et al*., 2017; Liebhold *et al*., 2017). A comprehensive insight into forest ecosystems at multiple scales is critical for formulating targeted, holistic and effective strategies for environmental conservation, climate change mitigation and adaptation. While current forest pathology research often focuses on ecosystem or global scales, there is a significant gap in knowledge at the microscale, such as host–pathogen interactions, microbiome functions, cellular microbial dynamics and gene functions within forest pathogen systems.

To elucidate microscale biological processes at the molecular level, contextualize them within broader frameworks and establish fundamental biological principles, experimental model organisms have historically been essential (Fields & Johnston, 2005). Classical *sensu stricto* model organisms, such as *Neurospora crassa*, *Saccharomyces cerevisiae*, *Arabidopsis thaliana*, *Caenorhabditis elegans* or *Drosophila melanogaster*, have provided a foundation to unlock our understanding of the biological world, including broad and general topics, such as the genetic code, gene regulation, cell cycle, circadian rhythms or embryonic development (Beadle & Tatum, 1941; Jacob & Monod, 1961; Hartwell *et al*., 1974; Nüsslein-Volhard & Wieschaus, 1980; Sulston *et al*., 1983; Kobilka *et al*., 1988; Hardin *et al*., 1990; Dunlap, 1999). In plant pathology and related disciplines, more field-specific experimental model systems have been established, such as *Magnaporthe oryzae*, *Ustilago maydis* or *Botrytis cinerea*. These systems have enabled significant advancements in understanding general aspects of host–pathogen interactions, such as infection strategies, effector biology and plant immune responses (Dean *et al*., 2012; Perez-Nadales *et al*., 2014; Kamoun *et al*., 2015).

There is ongoing debate about what constitutes a true 'model organism'. Some authors argue that only classical models with broad, generalizable insights qualify, while others contend that specialized models within specific fields, such as plant pathology, should also be included in this category (Gest, 1995; Bolker, 2009; Ankeny & Leonelli, 2011; Russell *et al*., 2017; Larraín, 2024). It is important to recognize that even the *sensu stricto* models initially underwent stages of development as experimental systems focused on specific questions or contexts. Over time, their use has transcended their original scope, providing insights that extend well beyond their own biology (Davis, 2004). Similarly, more applied or field-specific models serve as critical intermediaries toward developing generalizable biological principles. These models not only generate valuable insights for their respective fields but also contribute to broader scientific knowledge by connecting specialized research to universal biological frameworks. In this review, we therefore refer to all such systems – from classical, broad model organisms to more applied or field-specific models – as 'model organisms'. This inclusive definition acknowledges their collective role in advancing our understanding of biological processes and fostering connections across diverse scientific communities.

While research on existing plant pathology model systems has greatly advanced our understanding of plant–pathogen interactions, these findings often cannot be directly applied to forest pathogens due to significant differences in ecological complexity, host diversity and the life cycles of forest pathogens compared to agricultural model systems. The current increasing focus on forest health has highlighted a major gap in comprehensive methodologies within this field, especially when compared to the well-established frameworks of agricultural plant pathology, which developed robust experimental systems years ago and continuously integrate novel methodologies. In direct comparison, forest pathology has lagged behind for decades. A key strategy to address this gap is the development of specific forest pathology experimental models, which will enable faster and deeper insights into the molecular processes underlying interactions in these ecosystems, particularly for fungi and oomycetes. Integrating this knowledge with studies on broader spatial and temporal scales will be essential for driving innovation, improving predictions and enhancing protection efforts.

Here, we argue that the forest pathology research community, along with its funders, must urgently unite around the shared goal of developing a unified model system to drive progress in the field. Establishing such a model system should be more feasible and efficient than ever, given rapid technological advancement and interconnectivity, broad methodologies, such as genome sequencing, omics technologies and gene-editing tools, that can be swiftly adapted to new species, as well as our experience with historical model systems. Here, we propose a framework for such a process that draws on the evolution of model systems in other disciplines, particularly general plant pathology, while incorporating key developments and existing work specific to forest pathology.

The role of model organisms in advancing multidisciplinary research

The remarkable effectiveness of model organism research in advancing knowledge is based on a multidisciplinary scientific community gathering around their shared, standardized use. Focusing on one organism facilitates the integration of various disciplines and supports comparative research. For instance, thousands of researchers world-wide utilize *S. cerevisiae*, exploring a myriad of questions from diverse perspectives (Gaikani *et al.*, 2024). This consolidation of expertise and viewpoints fosters an understanding of the organism as a whole and its relationships with the environment. While knowledge gained from model systems does not represent all related biological systems, the insights obtained from studying these specific organisms serve as a basis for confirmation of general principles or their variations in other relevant target species in native environments (Jaspers *et al.*, 2019).

While a central objective of model organisms is to compress temporal and spatial scales, they are not intended to replace existing approaches. For example, fieldwork remains fundamental for capturing the epidemiology, diversity and complexity of ecosystems and for generating valuable hypotheses. Instead, model systems serve as a complementary framework, enabling researchers to test these hypotheses under controlled conditions and to contextualize new knowledge. Model organisms represent a deliberate abstraction of reality. By simplifying complex biological systems, they allow researchers to isolate and investigate key elements critical to understanding the underlying mechanisms of life. Without this abstraction, the accumulation of data from diverse and complex systems often fails to produce actionable insights. Models provide a reliable baseline against which the variability and complexity of real-world systems can be contextualized and contrasted. The standardization of a model organism can anchor findings and facilitate their interpretation within the broader landscape of biodiversity. In forest pathology, such model organisms are still lacking as part of a holistic research strategy that enables the standardized testing of scientific hypotheses derived from other existing approaches.

Experimental model systems have advanced the field of plant pathology

Although model organisms are still lacking in forest pathology, established fungal models have proven indispensable as 'engines of scientific insight' in related fields (Yarden, 2016). A promising approach to developing forest pathology models could be to draw on existing plant pathology models, which have been instrumental in advancing our understanding of plant–fungus and oomycete interactions over the years. Some of the best studied systems include *Magnaporthe oryzae* (Eseola *et al.*, 2021), *Fusarium oxysporum* (Di Pietro *et al.*, 2003; Michielse & Rep, 2009; but see Lombard *et al.*, 2019 about taxonomy), *Fusarium graminearum* (Goswami & Kistler, 2004), *Botrytis cinerea* (Williamson *et al.*, 2007), *Fulvia fulva* (syn *Cladosporium fulvum*) (Thomma *et al.*, 2005; Mesarich *et al.*, 2023), *Ustilago maydis* (Brefort *et al.*, 2009), *Zymoseptoria tritici* (Orton *et al.*, 2011) and *Phytophthora infestans* (Birch & Whisson, 2001) (Dean *et al.*, 2012; Kamoun *et al.*, 2015).

These systems have been crucial in addressing fundamental questions about fungal host plant invasion, colonization and immune evasion. Key concepts revealed through fungal models include the roles of cellular signaling pathways and secreted effector proteins in manipulating host plant responses, as demonstrated in *U. maydis* (Brefort *et al.*, 2009), *P. infestans* and *Phytophthora sojae* (Kamoun, 2006), *F. fulva* (Thomma *et al.*, 2005; Mesarich *et al.*, 2023), *F. oxysporum* (Di Pietro *et al.*, 2003) and *M. oryzae* (Stergiopoulos & de Wit, 2009; Oliveira-Garcia & Valent, 2015). As another aspect of the host–parasite arms race, recent work on *B. cinerea* has unveiled the complex fungal mechanisms employed against plant chemical defenses (You *et al.*, 2024). Additionally, research on these pathosystems has elucidated phenomena such as the 'two-speed genome' and its role in the evolution of plant pathogen genomes (Raffaele & Kamoun, 2012; Dong *et al.*, 2015), including the function of dispensable or accessory chromosomes, as observed in *F. oxysporum* (Ma *et al.*, 2010) and *Z. tritici* (Feurtey *et al.*, 2023). All of these advances relied on the combination of extensive methodologies developed by research communities, including genomics, transcriptomics, proteomics, reverse and chemical genetics, cell biology, advanced imaging and virulence assessments, both *in planta* and *in vitro*. Simply put: only when a broad range of standardized experimental methods is available for the same organism, as with model organisms, can they be combined to address complex questions. The mentioned examples of plant pathology models demonstrate both what can be achieved and what is required to develop model systems in forest pathology.

Why do we need a model system for forest pathology?

The plant pathogen models mentioned earlier primarily affect food crops and annual plants, making them insufficient for representing the specific features of forest pathogens. The host plants of forest pathogens, mainly trees and shrubs, along with their ecosystems, display distinctive structural and biological characteristics, which create unique conditions for host–pathogen interactions.

A key distinction is the longevity of trees compared to other well-studied host plants. This longevity underscores their remarkable resilience to environmental stress and pathogens, yet it also results in very slow genetic adaptation (Thomas, 2000; Matyssek, 2012). Tree-associated microbial communities evolve and interact with each other, their environment and the host plant also over extended periods (Terhonen *et al.*, 2019). Latent pathogens can persist within the host for long durations, eluding the plant's immune system until a stress-induced disease outbreak occurs (Slippers & Wingfield, 2007). A key challenge in developing model systems for forest pathology is therefore to shorten the experimental timeline without compromising the applicability of laboratory-generated data to natural settings.

Another crucial characteristic of trees is their distinctive anatomy, marked by pronounced secondary growth and a significant proportion of dead tissue, which requires protection from decomposing microorganisms. Tree-specific defense strategies include prominent and thick bark and resin ducts. Consequently, trees provide a different environment and nutrient source for pathogens compared to herbaceous plants (Thomas, 2000; Matyssek, 2012). Therefore, forest pathology research necessitates models that better capture these unique characteristics while considering space constraints, often in glasshouses that are difficult to secure for quarantine pathogens. So far, such a unified and organism-focused approach does not exist in this field.

Amidst the rapidly escalating global forest health crisis, numerous authors highlight a profound disconnect between policy, funding and the capacity to address these challenges (e.g. Wingfield *et al.*, 2015; Williams *et al.*, 2023). Alarmingly, major economies like the United States have experienced a decline in both capacity and funding since the 1980s (Hadziabdic *et al.*, 2021). These papers, representing a broader discourse, highlight the potential of emerging technological tools and emphasize the need for the next generation of scientists to integrate these innovations with traditional approaches to address the escalating crisis in forest health. We strongly support this perspective and propose that a comprehensive forest pathology model system could serve as a key tool to meet this challenge. Such a system, which bridges knowledge across disciplines, fosters technological advancements and generates innovative solutions, could not only attract increased funding and inspire a new generation of students, but also bolster the case for establishing dedicated faculty positions in forest pathology.

The development of model systems for forest pathology

When evaluating individual species as potential model systems, it is essential to ask: what features should a model system for tree and forest pathology possess? Insights from existing plant pathology models point to several key characteristics that are critical for developing effective experimental plant pathosystems. Building on this foundation, we suggest adapting the framework proposed by Feder & Mitchell-Olds (2003) for ecological genomics to guide the selection and development of model organisms in forest pathology (Fig. 1). Such a framework would support a more deliberate and question-driven choice of model systems. Important aspects to consider include experimental feasibility, standardized methods, the pathosystem context and the research community with its available resources.

Experimental feasibility

A foundational requirement for any model system in forest pathology is its experimental tractability. This encompasses practical considerations, such as generation time, growth conditions, laboratory propagation methods, quarantine status, host cultivation and the development of reliable infection assays. A key feature of robust model systems is genetic tractability, which enables the testing of hypotheses and the investigation of gene and protein function. This requires well-established protocols for genetic transformation and targeted gene modifications. The widespread adoption of novel gene-editing tools in fungal species has significantly simplified this process compared to the past.

Standardized methods

Standardization is a cornerstone in the development of effective model systems, ensuring that experiments are replicable, results are comparable and findings can be integrated across different research groups. This is essential for promoting collaboration within the broader scientific community and advancing collective knowledge. Key elements of standardization include selecting a designated reference strain, establishing consistent cultivation and sporulation conditions and developing uniform pathogenicity assays. However, achieving these standards is a significant challenge, as it requires the research community to come together and agree on these key issues. The process demands careful deliberation, iterative refinement and consensus-building, as researchers from diverse backgrounds must align on the best practices and protocols. Over time, this collaborative effort will lead to the establishment of robust, reliable models that can be widely adopted across the field.

Pathosystem context

For a forest pathology model system to be effective, it must incorporate pathogens that are nonquarantine, globally accessible and easily transferable across research settings. This ensures the model system can be widely used by the scientific community, promoting robust data integration and collaborative research. Additionally, selecting a pathogen species within a group of closely related pathogens can facilitate evolutionary comparisons and help validate discoveries across related systems.

Equally important is the choice of host plant species. The ideal host should have a relatively short lifecycle, rapid growth in

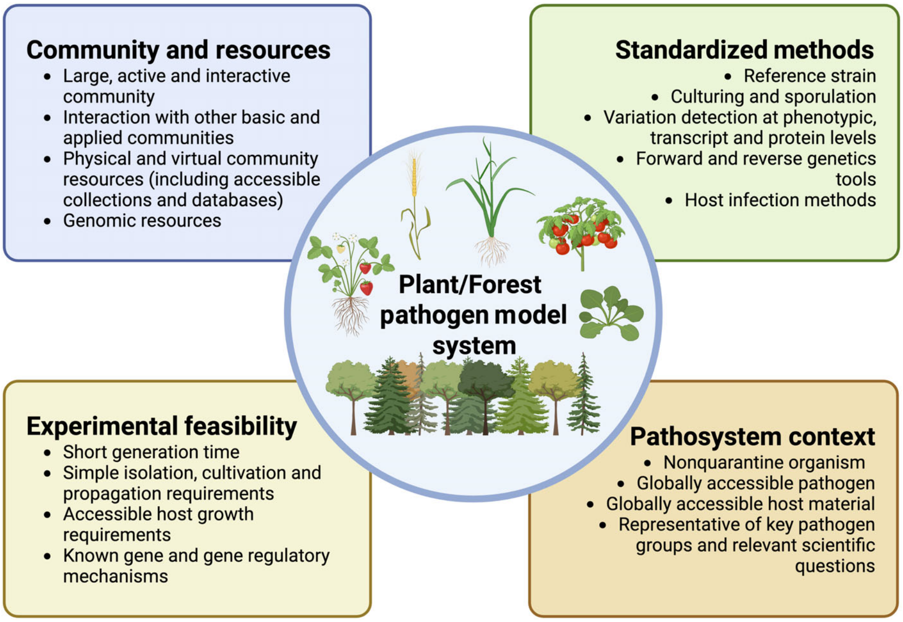

Fig. 1 The elements of a general plant pathology model system, inspired by Feder & Mitchell-Olds (2003) and adapted by considering lessons from existing plant pathology model organisms, which provide a framework for the development of forest pathology model systems. These include general elements of the community and resources, standardization, experimental feasibility, as well as the specific elements to consider in the context of a plant pathogen system and are discussed in more detail in the text. Created in BioRender (https://BioRender.com/55oriy4).

confined spaces (e.g. magenta boxes or similar equipment) and the ability to produce clonal material. It should also be globally accessible, with material available without quarantine restrictions. Genetic factors, such as aging (e.g. in conifers) and compatibility with gene-editing systems, should also be considered to support comprehensive investigations of host–pathogen interactions. An extensive amount of work has been done on the interaction between *Populus* and various of its associated pathogens and broader microbiome, offering a compelling system to consider for future work (Zeng *et al*., 2023). *Populus* is already a model system for woody plants, given its rapid growth, easy propagation (including widely available clones), compact genome, genetic tractability among other traits (Jansson & Douglas, 2007).

Steps toward developing other experimental tree host-pathogen/microbiome systems can be seen in Vivas *et al.* (2017) who studied host maternal effects on the microbiome of *Eucalyptus* seedlings in confined spaces. In the series of studies examining the effect of endophytic species on the pathogenicity of *Hymenoscyphus fraxineus* in *Fraxineus excelsior*, the authors developed axenic cultivation techniques for the host plant in laboratory settings (Halecker *et al.*, 2020; Demir *et al.*, 2024). In two recent studies, we developed a sporulation protocol, a transformation system, a time- and space-efficient laboratory-scale infection assay and cell biology tools for the *Diplodia sapinea*–*Pinus* interaction, enabling the study of gene/protein function, developmental processes and infection mechanisms (Oostlander *et al.*, 2023, 2024). While these systems all need further development to become broadly used experimental models, they illustrate potential starting points for the development of such model systems.

Community and resources

The development of a robust forest pathology model system depends not only on biological and experimental considerations, but also on the strength and cohesion of the research community. A large, active and interactive community is essential to drive progress, ensure continuity and foster innovation. Success ultimately depends on a well-established and adequately sized community working collaboratively to develop the necessary infrastructure and integrate molecular system data using standardized methods and strains. This includes strong connections with related basic and applied research communities, ensuring that insights and tools are transferable across disciplines.

To support this effort, both physical and virtual community resources are needed – such as accessible and well-maintained strain collections, shared genomic resources and curated databases that compile experimental protocols, phenotypic data and gene annotations. Regular meetings, shared platforms for communication and collaborative training opportunities help maintain momentum and ensure inclusivity. A collaborative ethos promotes the exchange of data and resources even before publication and regular meetings support dialogue and coordination of research activities, including joint efforts to secure sufficient research resources (Rhee, 2004; Ankeny & Leonelli, 2011; Yarden, 2016).

Current status

Some experimental organisms are already being used in forest pathology to address research questions. These organisms represent an important step toward developing such a model. The current best studied systems in tree or forest pathology based on publication records (Fig. 2) include the oomycetes *Phytophthora cinnamomi* (Hardham & Blackman, 2018) and *Phytophthora ramorum* (Grünwald *et al.*, 2008) (both with wide host ranges), as well as ascomycetes fungi, such as *Cryphonectria parasitica* on *Castanea* (Rigling & Prospero, 2018), *Ophiostoma ulmi* and *O. novo-ulmi* on *Ulmus* (Kirisits, 2013), *H. fraxineus* on *Fraxinus* (Combes

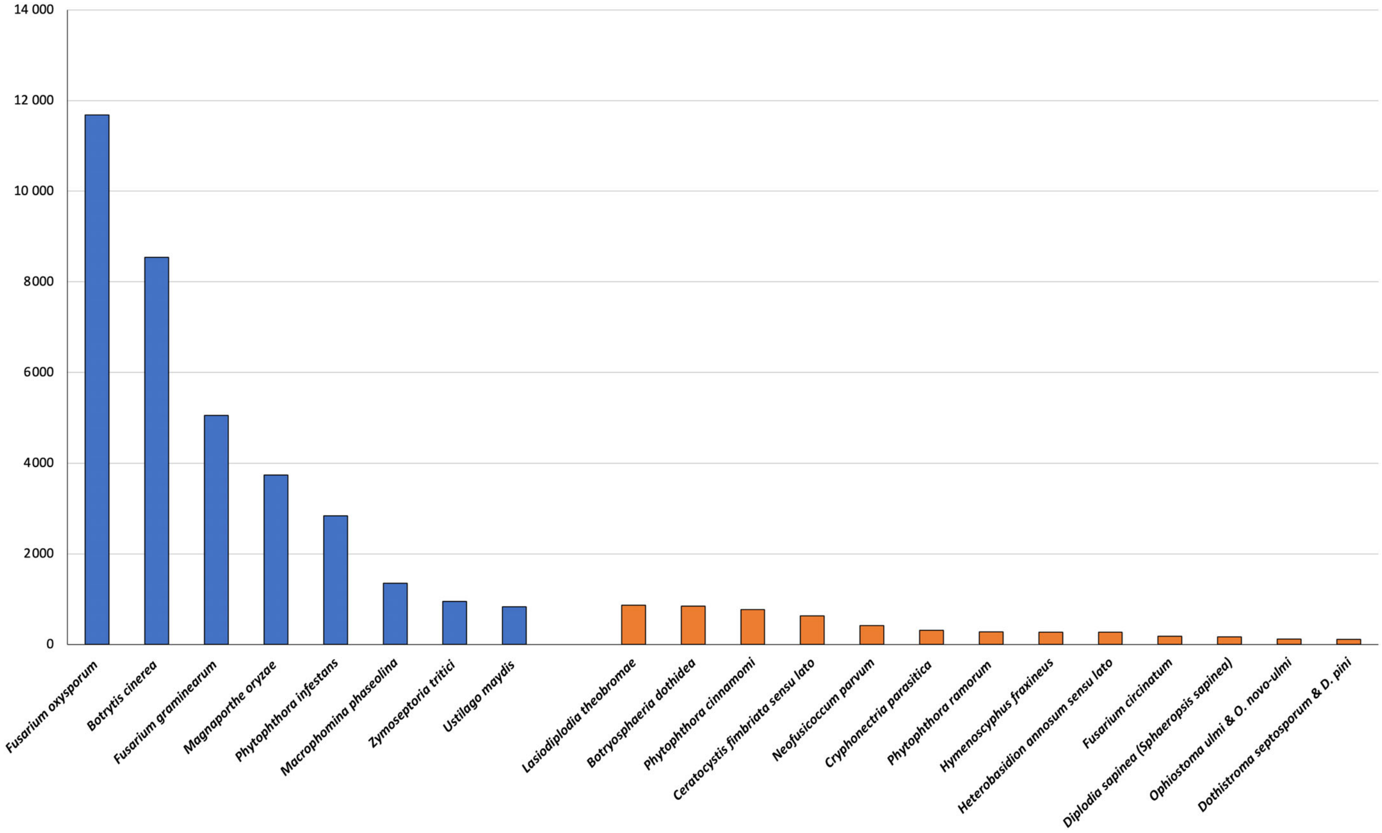

Fig. 2 Publications recorded in the Web of Science (all databases) for various plant pathogens (using the species name in the title, abstract and keywords) from 2019 to the present to represent the most recent trends (accessed March 2025). Pathogens of annual crops are blue and forest pathogens are orange.

et al., 2024), *Fusarium circinatum* on *Pinus* (Drenkhan *et al.*, 2020), *Ceratocystis fimbriata sensu* lato on various gymnosperms (Alizadeh *et al.*, 2024), *Melampsora larici-populina* and *Sphaerulina musiva* on *Populus* (Zeng *et al.*, 2023) and *Dothistroma septosporum* and *D. pini* on conifer trees (Drenkhan *et al.*, 2016), as well as members of the *Botryosphaeriaceae* (e.g. *Botryosphaeria dothidea*, *Lasiodiplodia theobromae* and *Neofusicoccum parvum* on various angiosperm hosts and *Diplodia sapinea* on gymnosperms) (Marsberg *et al.*, 2017; Batista *et al.*, 2021; Ma *et al.*, 2024; Wingfield *et al.*, 2025). Amongst the Basidiomycetes forest pathogens, *Heterobasidion annosum sensu* lato complex (*H. annosum*, *H parviporum* and *H. abietinnum* in Europe and *H. irregulare* and *H. occidentale* in North America) is best represented in literature (Garbelotto & Gonthier, 2013; Kovalchuk *et al.*, 2022). However, even the best studied of these systems (*L. theobromae*) pales in comparison to the resources being spent on plant pathogens of monocots and perennial agricultural crops (Fig. 2).

Applying the above-mentioned framework of criteria to the above-mentioned existing experimental systems in forest pathology reveals that, in addition to the relatively small research communities working on these pathogens, many tree pathogen systems lack several of the key features required for effective model systems. While genomic resources are now available for most of these fungi, forward and reverse genetics systems for studying gene function are often absent. Consequently, there remains a scarcity of gene function and gene regulatory information for many of these systems. Furthermore, some are hindered by quarantine status in certain countries, limiting the regions and types of research that can be conducted. Few of these systems offer easy-to-use, standardized methodologies, including plant access and growth requirements, which are likely the main barriers preventing broader basic and applied research community involvement. Other key steps include agreeing on a reference strain, establishing standardized cultivation and sporulation conditions and developing uniform pathogenicity assays.

The existing productive and competitive research communities must continue collaborating by establishing shared databases, holding regular meetings and intensifying efforts to secure joint research funding for developing these systems and resources. We do not intend to propose a specific organism or group of organisms for development into a model system here. Rather, our goal is to stimulate a discussion about the critical need for model organism research in forest pathology and the necessary steps that must be taken to establish such systems.

Model systems can advance the understanding of pathobiomes in forest pathology

An often overlooked impact of changing environmental conditions is their effect on forest pathogens in the context of their interactions with microbial communities on the host and in the environment; referred to as the pathobiome (Brader *et al.*, 2017; Bass *et al.*, 2019). Changes in the composition and equilibrium of these communities are likely to significantly impact the resilience of forest ecosystems (Terhonen *et al.*, 2019; Baldrian *et al.*, 2023). In addition, pathobiome research on agricultural plants and plant model systems revealed that the plant microbiome coevolves with the host and influences its performance and that it is integrally linked to plant immunity (termed microbe-mediated immunity; MMI) (Mesny *et al.*, 2023; Ruiz-Bedoya *et al.*, 2023a). These findings offer alternatives to traditional resistance breeding by leveraging microbial ecological complexity. When considering the future of model systems, it is therefore important to move beyond single pathogen systems and incorporate the broader ecological complexity of pathogen-microbiome interactions.

Studies on the use of MMI increasingly rely on the use of Synthetic Communities (SynComs) to model microbe–microbe and host–microbe interactions and enable detailed characterization of microbial dynamics and their impact on plant health, although mostly still using bacteria (Shayanthan *et al.*, 2022; Martins *et al.*, 2023; Northen *et al.*, 2024). Studies with SynComs have, for example, demonstrated the role of commensal microbes in immune priming through induced systemic resistance, synergistic pathogen defense and recruitment of disease-protecting microbes (Berendsen *et al.*, 2018; Liu *et al.*, 2021; Song *et al.*, 2021; Shalev *et al.*, 2022). Additionally, this line of research has highlighted the potential for inter-kingdom interactions, where microbial consortia can confer antifungal protection or, conversely, enhance pathogen susceptibility under certain conditions (Seybold *et al.*, 2020; Li *et al.*, 2021; Ruiz-Bedoya *et al.*, 2023b). These studies reveal complex cooperative and competitive dynamics within microbial populations, influencing collective virulence and suggesting innovative plant disease management strategies.

The studies to date on the detailed mechanisms underlying MMI are almost all based on model systems and agricultural plants. The microbial biodiversity involved, host structural considerations and the nature of the microbial interactions given the longer life span of trees, however, are all expected to be unique. While there are numerous studies on the microbiome diversity in trees and factors influencing this diversity, including on the interactions between microbiomes and tree health (Asiegbu & Kovalchuk, 2021; Xiong *et al.*, 2023), studies on SynComs to unravel the underlying mechanisms needed to apply these concepts for tree health management are rare. A series of studies mentioned earlier that used axenic, containerized *F. excelsior* seedlings to study endophyte–pathogen (*H. fraxineus*) interactions comes closest to our knowledge to such studies (Halecker *et al.*, 2020; Demir *et al.*, 2024). This is perhaps not surprising given the complexity of doing such research on tree systems and provides a compelling case for the need of a forest pathology model system, which also enables standardized analysis of microbiome role and function in plant health and development.

Conclusion

The global forest health crisis demands urgent and intensified research in forest pathology. Given the urgency of the challenges facing forest ecosystems, we believe the time is ripe – and the need is pressing – for the forest pathology research community to unite and develop comprehensive model systems for advancing the field. Recent technological advances and the increasing ease of developing global networks make this goal more attainable than ever before. Existing experimental systems can serve as a foundation for this development, and we offer key considerations to guide its progress.

It is important to remember that model organisms serve as both concrete examples and representatives of a larger collective (Ankeny & Leonelli, 2011; Bertile *et al.*, 2023). These models often lead to groundbreaking, disruptive discoveries, the significance of which emerges through comparative work with other organisms. Such a system holds the potential to integrate the existing body of field and biological research in forest pathology with the power of a unified experimental model, thereby promoting molecular forest pathology and connecting a broader community not currently involved in forest pathology, rather than replacing existing approaches.

Developing a model system(s) for forest pathology that engages a global community of researchers presents significant opportunities to advance the field, similar to the impact of model systems in agriculture and human health. To achieve this, the research community should focus on key species and build collaborative resources to facilitate studies across a much broader range of laboratories than is currently the case. Achieving these goals is neither a singular decision nor a simple process. It requires years of iterative development and rigorous evaluation to identify and establish suitable experimental organisms as model systems. It will also require that funding bodies recognize the need for consistent, long-term funding behind fundamental research on experimental systems in forest pathology.

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Competing interests

None declared.

Author contributions

AO, AF and BS contributed equally to the conceptualisation, writing and editing of the manuscript.

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