



# Invasion Frameworks: a Forest Pathogen Perspective

Trudy Paap<sup>1</sup> · Michael J. Wingfield<sup>1</sup> · Treena I. Burgess<sup>1,2</sup> · John R. U. Wilson<sup>3,4</sup> · David M. Richardson<sup>4</sup> · Alberto Santini<sup>5</sup>

Accepted: 22 November 2021 / Published online: 21 February 2022  
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## Abstract

**Purpose of Review** Within the discipline of invasion science, researchers studying different taxonomic groups have developed distinct ways of investigating the phenomenon of biological invasions. While there have been efforts to reconcile these differences, a lack of knowledge of diversity, biogeography and ecology hampers researchers seeking to understand invasive microorganisms, including invasive forest pathogens (IFPs).

**Recent Findings** Advances in molecular technologies such as gene and genome sequencing and metagenomics studies have increased the ‘visibility’ of microorganisms, providing opportunities to better integrate forest pathology and invasion science. The two fields have much to gain from closer collaboration.

**Summary** We propose a modified version of the Unified Framework for Biological Invasions to accommodate IFPs, recognising the challenges and limitations, and suggest options for tackling these issues. We explore the pathways by which IFPs are transported and in doing so highlight the need for the refinement of current pathway frameworks to better accommodate IFPs. With a clearer understanding of how microorganisms move around and the stages they pass through to become invasive, we hope that forest pathologists will better understand how and why invasions occur and, importantly, where, when, and how invasions can be stopped or mitigated. We call for a broader incorporation of ecological and evolutionary concepts to address the complex challenges of identifying and managing IFPs.

**Keywords** Biological invasions · Coevolution · Emerging diseases · Invasion science · Invasive forest pathogens · Microbial invasions · Tree disease

## Introduction

Biological invasions present a growing threat to global biodiversity, ecosystem services, economies and human health [1]. The concept of biological invasions is not limited to particular taxonomic groups. However, invasion science has focused mostly on plants and animals [2, 3], and microorganisms are relatively poorly represented in the invasion science literature [3–5]. This is despite pathogenic microorganisms consistently being ranked amongst the most damaging invasive species [6, 7] and the increasing threats they pose to human health, domesticated animals and crops, and wildlife [8, 9, 10•].

Invasive forest pathogens (IFPs), in particular, can completely alter natural, planted and urban forests and woody ecosystems. Well-known examples of disastrous disease epidemics following the arrival of IFPs include chestnut blight (caused by *Cryphonectria parasitica*) in the USA and Europe [11], ash dieback (*Hymenoscyphus fraxineus*) in Europe [12],

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This article is part of the Topical Collection on *Forest Pathology*

✉ Trudy Paap  
trudy.paap@fabi.up.ac.za

- <sup>1</sup> Department of Biochemistry, Genetics and Microbiology, Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria, South Africa
- <sup>2</sup> Harry Butler Institute, Murdoch University, Murdoch 6150, Australia
- <sup>3</sup> South African National Biodiversity Institute, Kirstenbosch Research Centre, Cape Town, South Africa
- <sup>4</sup> Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa
- <sup>5</sup> Institute for Sustainable Plant Protection, National Research Council, 50019 Sesto Fiorentino, Italy

**Fig. 1** Examples of impacts caused by invasive forest pathogens—**A** an American chestnut stand gutted by the chestnut blight pathogen, *Cryphonectria parasitica* (Library of Congress, Prints & Photographs Division, Reproduction number HAER VA,70-LURA.V,4—97); **B** Ash dieback in Europe, caused by *Hymenoscyphus fraxineus*; **C** *Austropuccinia psidii* causing myrtle rust on *Myrtus communis* in South Africa; a serious threat to European myrtle; **D** *Phytophthora cinnamomi* devastating Proteaceae-dominated ecosystems in southwest Western Australia



*Austropuccinia psidii* (cause of myrtle rust) in Australian rainforests [13], and *Phytophthora cinnamomi* in southwest Australia [14] (Fig. 1). As a result of these and other diseases, entire tree species have been functionally eliminated from landscapes. Direct and indirect effects on communities follow, including significant alteration in species richness and abundance, as well as the loss of various ecosystem services.

Within the discipline of invasion science, researchers studying different taxonomic groups and different environments have developed distinct ways of investigating invasive alien species (IAS). Efforts have been made to reconcile these differences, notably in the proposed Unified Framework for Biological Invasions (the Unified Framework) [15••], which merges definitions and processes for studying plant and animal invasions. However, practical issues arise when applying the framework to microorganisms [3]. Forest pathologists (and more broadly microbiologists) are generally absent as authors from the literature in which the frameworks most widely used for studying invasions have been proposed. That said, the idea of pathogens as invasive species is not new,

and the microbial dimension of biological invasions has been explored in several reviews. However, these have generally been written by microbiologists or, where dealing specifically with forest pathogens, forest pathologists [6, 16, 17•, 18]. Similarly, several recent papers [8, 10•, 19] have compared the study and management of emerging infectious diseases (EIDs) with that of biological invasions. While the two fields have worked chiefly in parallel, they have similar management goals.

Microbial invasions have been described as one of the most pressing topics facing invasion science [8, 20••], and collaboration between the two fields is crucial to address the challenge. This is especially in light of the continued increase in global connectedness, and the alteration of biological systems—factors which contribute to all types of biological invasions (including IFPs). We believe that the key to managing pathogens is understanding them as invasive species. To this end, we present a modification of the Unified Framework [15••] to accommodate forest pathogens.

## Box 1: Glossary

**Biological invasions:** the phenomenon of and suite of processes involved in determining the transport of organisms to sites outside their native range by human activities and the fate of the organisms in their new ranges [21].

**Emerging infectious disease (EID):** an infectious disease appearing in a population for the first time or that may have existed previously but that is increasing rapidly in incidence or geographic range.

**Invasive alien species (IAS):** self-sustaining (naturalised/established) population of a species, accidentally or intentionally introduced by human actions, to an area outside of their native geographic range, into an area where they are not naturally present. While not all definitions include impact, others specify IAS cause, or are likely to cause, socio-cultural, economic, or environmental harm or harm to human health.

**Invasive forest pathogen (IFP):** A pathogenic microorganism (a species, subspecies, race, or forma specialis) introduced by human actions to an area outside its natural distribution, where it behaves as an agent of disease on native or alien trees or shrubs.

**The proposed Unified Framework for Biological Invasions (the Unified Framework):** developed by Blackburn et al. [15••], the Unified Framework describes the introduction-naturalisation-invasion continuum. The framework aimed to link those previously developed by botanists and zoologists, to provide a single conceptual model that could be applied to all human-mediated invasions, regardless of taxon, location or realm.

**The Convention on Biological Diversity (CBD) introduction pathway categorisation scheme:** a hierarchical scheme that categorises the pathways along which alien species are moved from one biogeographical region to another. It has six main categories based on the 2008 framework of Hulme et al. [22], and 44 additional sub-categories that were included so the scheme aligned better to existing schemes. For a guide to interpreting the scheme, see Harrower et al. [23]. The intention of the scheme is to facilitate the monitoring, management, and regulation of introduction pathways.

## Challenges to understanding forest pathogen invasions

There are several key challenges to studying microorganisms as invasives. First, the diversity of microbial taxa is vast, with many taxa yet to be discovered and described [4]. Second, even if a name has been ascribed, there is often a lack of information on geographical origins. For example, the origin of *Ophiostoma ulmi* s.l. (causal agents of one of the most devastating tree pandemics, Dutch elm disease), introduced in Europe and North America in the early 1900s, remains unknown [24]. This means it can be impossible to separate native from alien ranges [25] hampering the search for potential biological control agents [26]. Third, the functional diversity of microorganisms is also vast, with numerous microbial

functional guilds, many different life-history strategies, and a plethora of different traits.

The fourth key challenge is that of detection. Invasive microorganisms are often only perceived when their impacts become palpable. In practice this is usually not an issue—severe disease outbreaks by native pathogens under natural environmental conditions are rare, with coevolution between plant pathogens and their hosts, together with pressures from competition, predation, and parasitism, contributing to the stability of natural ecosystems [27]. Many IFPs did not cause severe disease in their native environment, or were even unknown to science before their arrival, establishment, and invasion in a novel environment. However, in recent decades, there has been a rise in emerging forest diseases caused by native pathogens. This is essentially due to breakdowns in ecosystem resilience due to global change drivers, including climate change, land use change, anthropogenic disturbance, and indeed other biological invasions [28]. Therefore, invasion events involving pathogens are challenging to predict [9].

Finally, the impacts of non-pathogenic microbial invasions are less apparent than those of pathogens and are often difficult to quantify. We recognise that of all the categories of microorganisms, pathogens (including IFPs) are amongst those most widely studied; the residency status (native or alien) is even less known for many other groups (e.g. endophytes, mycorrhizal fungi) [29].

Paap et al. [3] interrogated the history of the disciplines of forest pathology and invasion science, providing insights as to why the two fields have remained relatively unconnected. Forest pathologists have traditionally used the approaches from the broader field of plant pathology, with studies on IFPs often focused on controlling the observed disease problem rather than understanding the invasions. The fact that many contemporary forest pathologists have classical plant pathology backgrounds, rather than training in forestry or ecology, has influenced the focus and approach of their studies [3, 4]. In contrast, invasion scientists have tended to work within a paradigm focused on natural ecosystems and have focused mainly on animal and plant invasions. The presence of separate regulatory bodies established to deal with threats to plant health and threats to biodiversity has likely exacerbated this issue. The International Plant Protection Convention (IPPC) aims to prevent and control the introduction and spread of plant pests. While impacts on natural environments are considered, the emphasis of phytosanitary regulations remains largely

focused on plants of economic importance [9, 30, 31••]. The World Trade Organization (WTO) Agreement of the Application of Sanitary and Phytosanitary Measures (the SPS agreement) [32] primarily aims to minimise the disruption plant health regulation might impose on trade, by preventing countries from implementing protectionist trade barriers [30, 33, 34]. By contrast, the Convention on Biological Diversity (CBD) explicitly considers the natural environment and addresses IAS in the CBD Aichi Biodiversity Target 9 (<http://www.cbd.int/sp/targets/>). However, microorganisms remain significantly underrepresented in IAS databases. Consequently, alien pathogens affecting wildlife, including IFPs, have often fallen into the gaps between the regulatory bodies [9, 33].

## Barriers to disease development

There are three types of barriers limiting the potential of pathogens to cause severe disease outbreaks: geographical, environmental, and evolutionary. Although release from any one of these barriers can lead to disease development, the crossing of geographical barriers, by human-mediated dispersal, is recognised as the process that defines biological invasions [10•]. In crossing this barrier, opportunities arise for microorganisms to encounter naïve hosts lacking coevolved resistance. Essentially, release from the geographic barrier means that it is more likely that an evolutionary (compatibility) barrier can also be crossed. Evolutionary barriers may also be overcome when a host is planted outside its natural range, presenting opportunities for microorganisms native to the planted range to adapt to the novel host species, resulting in host jumps [35–37].

Global change factors, including habitat disturbance and climate change, are challenging the environmental barriers under which resistance has evolved. This leads to situations where native pathogens exhibit increased pathogenicity to coevolved hosts in their natural environment [38, 39]; in some cases, this results in severe disease outbreaks [40, 41]. The environmental barrier may also be crossed when a host is planted outside its natural range, should a coevolved pathogen also establish in this region (i.e. pathogen reunion). Under novel conditions, which may include monoculture plantings (particularly in the case of commercially planted species), the resulting environment may be conducive for disease to develop beyond levels encountered in the host/pathogen natural range [42].

Following the introduction of an alien pathogen, disease can develop: (1) on a coevolved alien host (pathogen reunion); (2) on a naïve alien host (host jump); (3) on an alien host (naïve and/or coevolved), with spill-over to a native host that cannot sustain the IFP population (i.e. if the alien host is removed the IFP will die out); (4) on alien and native hosts;

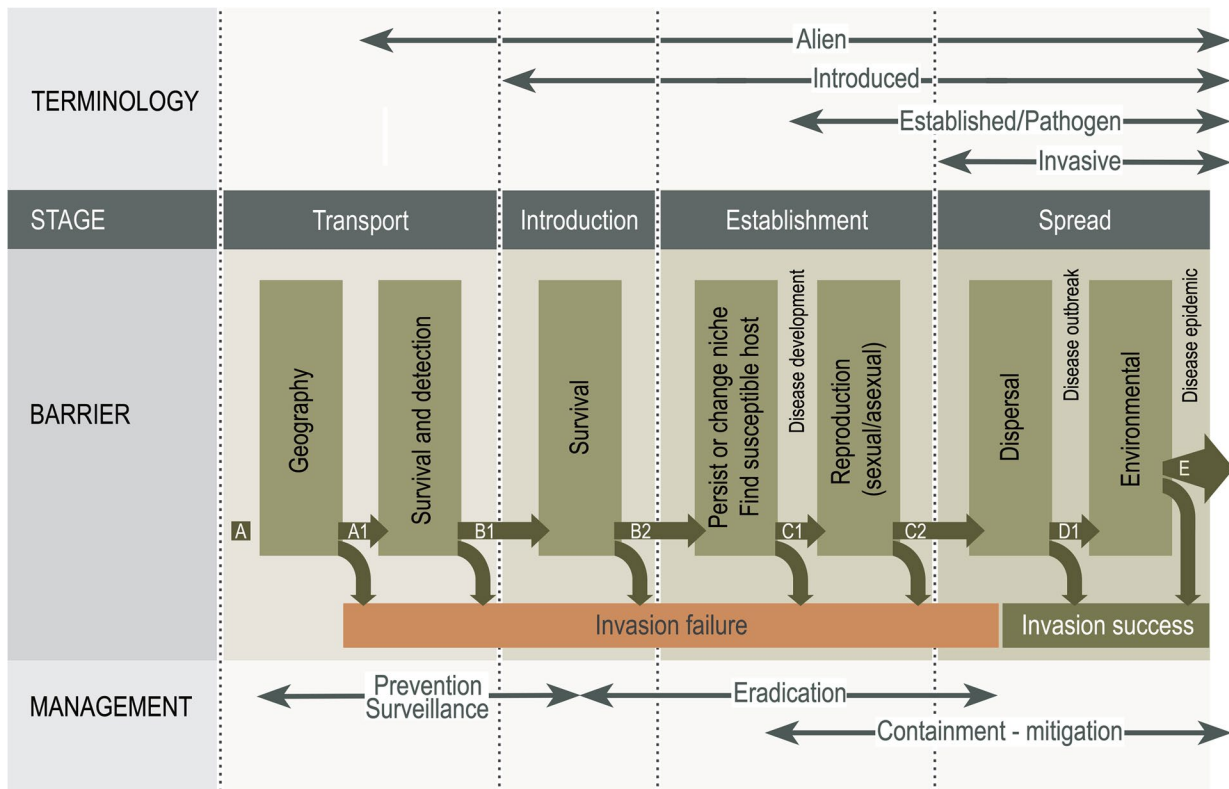
and (5) on a native host but not on an alien host. As such, the introduction of an IFP may result in different disease scenarios in different invaded regions. For example, *Fusarium circinatum* is considered to be one of the most important pathogens affecting *Pinus* seedlings and mature trees [43, 44]. In Spain, *F. circinatum* has impacted alien *P. radiata*, but also native *P. halepensis* and *P. pinaster* [45]. In South Africa, however, *F. circinatum* only causes disease in plantations of alien *Pinus* spp. [44]; the absence of native congeners means the pathogen has never jumped to native hosts. The likely disease scenario will thus largely be determined by whether the IFP is a generalist or specialist and, particularly in the case of specialists, the presence of native hosts with close phylogenetic relationships to the coevolved host, e.g. the devastating IFP *Cryphonectria parasitica* jumped from Asian to American and European *Castanea* spp. [11].

## Pathways for pathogen introduction

Harrower et al. [23] define introduction pathways as ‘processes that result in the introduction of an alien species from one geographical location to another’. Microorganisms, including IFPs, are generally introduced to novel regions via the two categories of unintentional transport: ‘contaminant’ and ‘stowaway’, as per the CBD’s introduction pathway categorisation scheme [46]. The main distinguishing feature between these two categories is whether or not the organism is biologically connected to the commodity with which it is transported. Organisms transported as contaminants interact directly with the commodity, i.e. are biologically connected, while stowaways use a vector to move between locations, without interacting with this vector [23].

Within these categories, several sub-categories, as described by Harrower et al. [23], accommodate microorganisms. Contaminant sub-categories include the following: ‘contaminant nursery material’, ‘contaminant on plants (except parasites, species transported by host/vector)’, ‘parasites on plants (including species transported by host and vector)’, ‘seed contaminant’, ‘timber trade’, and ‘transportation of habitat material (soil, vegetation)’. These sub-categories apply to microorganisms present in or on transported commodities and fungal mutualists of vectors such as ambrosia beetles (with the beetles themselves also present as either contaminants or stowaways). Specifically, translocation of microorganisms as contaminants can occur following translocation of a host plant or soil in which they are present as endophytes, saprophytes, pathogens, or mycorrhizae [47]. Microorganisms may also be contaminants of seeds [48, 49] or plant parts and other products [50].

Stowaway sub-categories include the following: ‘machinery/equipment’, ‘people and their luggage/equipment (in particular tourism)’, and ‘organic packing material (wood packaging)’. The most common examples of microorganisms present as stowaways include spores on tourist clothing



**Fig. 2** A proposed framework of the invasion process for forest pathogens. The framework follows the series of sequential stages (transport, introduction, establishment and spread) developed by Blackburn et al. [15••]. Each stage contains one or more barriers that must be overcome to transition through to the next stage. Invasive forest pathogens are microorganisms that have successfully passed each stage and/or barrier and spread throughout the recipient region. The arrows

indicate the progression of individuals. The alphanumeric codes associated with the arrows relate to the categorisation of microorganisms on the pathway to invasion success (outlined in Table 1, main text). Management options are presented according to the stage of invasion, and differing levels of impact are designated following transition across the barriers

[51] or in soil attached to footwear or equipment, e.g. tents, containers [52, 53]. The stowaway category also includes two hitchhiker sub-categories: ‘hitchhikers in or on airplane’ and ‘hitchhikers on ship/boat (excluding ballast water and hull fouling)’. However, Harrower et al. [23] specify that the hitchhiker pathway applies only to species interacting directly with the vessel (airplane or ship) itself, and not to species interacting with cargo, containers, packaging, people, or luggage transported by the vessel. This precludes the use of the hitchhiker sub-category for microorganisms. Of note is that the term ‘hitchhiker’ is commonly used by forest pathologists to refer to microorganisms, including pathogens, transported with asymptomatic plants [3, 47]. In this context, the term applies to microorganisms with a biological connection to the organism with which they are transported. Following the CBD pathway categorisation, this would align it with the contaminant pathway; however, there is no instance in the invasion terminology linking the term hitchhiker to this pathway.

Faulkner et al. [54] provide a broader critique of the CBD pathway categorisation. They highlight the need for

refinement of the sub-categories and suggest context-specific categories may be more effective in accommodating regional and taxon-level requirements [54]. We agree such a refinement should be undertaken for IFPs. This revision should also take into consideration the pathway terminology of the IPPC. Within a phytosanitary context, pathway is defined as ‘any means that allows the entry or spread of a pest’ [55]. However, there is currently a lack of standardised pathway categories, despite the provision for the identification of pathways in the frameworks for pest risk analysis [56–58] and the adoption of International Standards for Phytosanitary Measures (ISPMs) for several pathways recognised as high-risk for the movement of plant pests, e.g. ISPM 15, which provides treatment standards for wood packaging material [59], and ISPM 38 for the international movement of seeds [60]. A Focus Group on Commodity and Pathways Standards was established in 2018 [61], but to date there remains a lack of clear guidance with regards to pathway categories.

**Table 1** Categorisation scheme for the stages microorganisms pass to become invasive forest pathogens. We have proposed a link to the Darwin Core (a biodiversity data standard) based on the term `dwc:degreeOfEstablishment` as outlined in Groom et al. [98], noting that not all steps are analogous (denoted by NA)

Step	Explanation	Corresponding Darwin Core term
A0	Microorganisms in their native range	native
A1	Microorganisms in transit (as contaminants or stowaways in or on host plants, substrate or vector) moved beyond their native range	NA
B1	Microorganisms transported beyond limits of native range survive transport and escape detection/quarantine measures in non-native destination <sup>a</sup>	Captive, cultivated, released, failing (B1 only), or casual depending on location of the host or substrate
B2	Microorganisms survive in the non-native environment where introduced, remaining on the host or substrate with which they arrived and evade detection. No reproduction <sup>a</sup>	
C1	Microorganisms survive in the non-native environment where introduced, persist, or adapt to a new niche/environment and find a susceptible host by host jump or pathogen reunion. Establish as a pathogen. Reproduction may be occurring but only within the original host or substrate with which they arrived. Disease may develop on newly infected host <sup>a</sup>	reproducing
C2	Microorganisms survive in the non-native environment where introduced, reproducing and maintaining a self-sustaining population on a susceptible host or in non-native environment <sup>a</sup>	established
D1	A self-sustaining population, with individuals able to survive and reproduce on a susceptible host beyond the original area of introduction, giving rise to a disease outbreak <sup>a</sup>	colonising or invasive
E	Fully invasive pathogens, with individuals dispersing, surviving and reproducing at multiple sites across the introduced region, giving rise to a disease epidemic	widespreadInvasive

<sup>a</sup>Failure to pass the barrier may be a result of management efforts or inability to survive or reproduce in the non-native environment due to environmental constraints or lack of a suitable host (evolutionary constraints)

## Understanding the forest pathogen invasion process

Invasive forest pathogens (IFPs) are both invasive alien species (IAS) and emerging infectious diseases (EIDs). The terminology and frameworks of both EIDs and IAS should thus inform our understanding of IFPs. To this end, we examine the stages of disease emergence proposed by Hatcher et al. [62] and Dunn and Hatcher [33]; the proposed Unified Framework for Biological Invasions developed by Blackburn et al. [15••]; and the modification of the Unified Framework by Chapple et al. [63] that details the invasion process for IAS arriving as unintentional introductions. While focused on animals and their behavioural traits rather than microorganisms, Chapple et al. [63]’s modification accommodates several features observed in the invasion process of IFPs, due to their predominant arrival by accidental introduction.

Figure 2 presents our attempt to modify the Unified Framework to accommodate IFPs. We maintain the four stages (transport, introduction, establishment, and spread) outlined by Blackburn et al. [15••]. In addition, we consider impact a necessary component. While not all definitions of IAS include impact, with regard to IFPs, only when impact, i.e. disease development, is observed, is there evidence of the microorganism’s presence, leading to its detection and identification [3]. Table 1 describes the steps progressing through the barriers

of each stage, indicated by the alphanumeric codes in Fig. 2. We note that the barriers proposed in the Unified Framework overlap with the barriers to the development of EIDs. Details of the barriers to be overcome as an organism passes through the stages of invasion are described below.

### Stage 1: transport

The frameworks developed for EIDs [33, 62] replace the transport stage with ‘Contact’. They highlight several means by which contact can occur but ultimately describe the stage as contact between a reservoir and novel hosts. Because IFPs must undergo movement from a native to the non-native range, we retain the term ‘transport’ of the Unified Framework.

The first barrier is passed at the point where the microorganisms are in transit. In contrast to most plants and many animals, the movement of microorganisms is generally unintentional, either by the contaminant or stowaway pathways. Chapple et al. [63] introduce the term “uptake” to describe the process whereby individuals are ensnared as stowaways within a transport vector. While some microorganisms are transported as stowaways, many are biologically linked to their hosts and do not undergo the uptake step. Consequently, we utilise the geography barrier but do not specify the uptake stage of Chapple et al. [63].

As a consequence of their unintentional movement, the survival of microorganisms during transport is not ensured. Therefore, a second barrier exists: survival and detection. The organism must survive transport and escape detection and quarantine measures, including phytosanitary treatments, to pass the transport stage. Visual inspection can only detect microorganisms with a visible presence such as pathogens causing disease symptoms [64]. However, many microorganisms are present on or within plants or other substrates without any signs or symptoms. Furthermore, due to vast volumes of traded goods, it is only possible to inspect a fraction of consignments [34, 65]. While molecular assays can detect microorganisms in the absence of symptoms, with some arrays even developed to screen for multiple organisms simultaneously, these techniques can only be applied for known pathogens.

### Stage 2: introduction

The Unified Framework proposes a barrier for intentionally introduced organisms, where introduction requires escape from captivity or cultivation [15••]. They acknowledge unintentionally introduced organisms (including microorganisms) may skip this barrier and be directly released into the non-native environment, essentially bypassing the introduction phase. Chapple et al. [63] maintain a barrier for stowaways, ‘Disembarkation’. This is essentially the opposite of uptake, with individuals exiting the transit vector to enter the non-native environment. Dunn and Hatcher [33] equate spill-over of EIDs with the introduction stage of biological invasions. For IFPs, however, we consider the host jump (or pathogen reunion) step to occur post-introduction.

In our modified framework, we maintain the introduction stage of the Blackburn et al. [15••] framework, and we propose a second survival barrier. By overcoming this barrier, the organism is surviving in the non-native environment, although still attached to the host or substrate with which it arrived. Where an organism arrives in a symbiotic relationship with its host, i.e. the contaminant pathway, successful introduction may be dependent on the establishment of the host. In cases where the host dies, pathogen escape may still occur if the plant material is not appropriately contained or quickly destroyed. For organisms arriving with seeds, the ability to transfer from the seed to the seedling (vertical transmission) ensures their survival at this stage. Organisms arriving as stowaways must be able to persist as propagules in the non-native environment.

### Stage 3: establishment

Establishment requires an organism to persist in the non-native environment and may require the organism to

undertake a host jump or shift in the environmental niche. Where the non-native environment matches the native environment (e.g. similar temperature and moisture conditions), this may be an insignificant barrier for the organism to overcome. However, where the environment differs, the organism must be able to change its environmental niche. The second component of this barrier involves finding a suitable host. At this point, host jump (or pathogen reunion) has occurred, and we consider the organism to be in its role as a pathogen, with the evolutionary barrier to EIDs also overcome. Impact may be observed as localised disease development.

Blackburn et al. [15••] propose a second barrier to the establishment stage, i.e. reproduction. Once the pathogen has passed the first barrier, changing niche and/or finding a susceptible host, reproduction is not a strong limiting factor. However, the newly introduced pathogen may remain limited to an area as a result of environmental constraints. Similar to the Unified Framework, the reproduction barrier is important to the establishment of IFPs, with local environmental factors or host or habitat competency potentially limiting reproduction.

For EIDs, establishment is equated with persistence or local establishment in novel hosts [33, 62]. This is the case also for IFPs. As with other IAS and EIDs, establishment of IFPs is influenced by demographic, evolutionary and environmental factors. Microorganisms with complex life cycles (e.g. requiring insect vectors, alternate hosts) may fail to establish if they cannot adapt, i.e. find new vectors or hosts. Generalists and microorganisms with saprophytic stages or the ability to survive in the environment as durable spores may be more likely to establish [6, 47].

### Stage 4: spread

Having overcome the establishment barriers, and with reproduction leading to population increases, the first barrier to spread is encountered. As proposed by Blackburn et al. [15••], dispersal may be natural or human-assisted and gives rise to populations far from the original point of introduction. For EIDs, the spread stage matches that of IASs, with disease emerging in populations across a broad geographical range [33]. Once pathogens have passed this barrier, impact may become noticeable as a disease outbreak.

Chapple et al. [63] highlight how successfully established populations of unintentionally introduced species often experience a lag phase before spreading out across the non-native region. They provide several explanations for this delay in population spread, including the amount of time required for sufficient population growth, adaptation to the new environment, augmentation of genetic variation,

**Table 2** Management goals and strategies at the sequential stages of the invasion process of invasive forest pathogens, challenges to implementation of these measures, and potential solutions and areas of research need to address these challenges. Key references are provided for known examples and for literature discussing research needs

	Management goals and strategies	Challenges	Examples	Potential solutions/research needs
<b>TRANSPORT</b>	<p><b>Prevention and surveillance</b></p> <p>Early warning/horizon scanning</p> <p>Pest risk analysis</p> <p>Biosecurity</p> <p>Plant passports</p> <p>Quarantine</p> <p>Visual inspections/lab analyses/phytosanitary treatments</p> <p>Name based</p>	<p>Inconspicuous microorganisms escape visual detection</p> <p>IFP unknown to science prior to establishment in a novel environment and jump to naïve host lacking resistance genes</p> <p>Name-based biosecurity is reliant on robust and accepted taxonomy</p> <p>Variation in virulence between different strains/different mating types</p>	<p>Movement of <i>Phytophthora</i> spp. by nursery trade of infested asymptomatic plants [64]</p> <p>Chestnut blight caused by <i>Cryphonectria parasitica</i> in North America and Europe [11]</p> <p><i>Austropuccinia psidii</i> wrongly identified as the lesser pathogen, <i>Uredo rangelii</i>, in Australia. Incursion downplayed, quarantine response stopped after 9 days [99]</p> <p>Strain-related pathogenicity in <i>Diplodia corticola</i>, canker pathogen of oak [100]</p>	<p>Strengthen biosecurity/quarantine [65, 87]</p> <p>Sentinel plantations in country of export [82]</p> <p>Management of high-risk pathways [65]</p> <p>Rapid molecular diagnostics [77]</p> <p>Studies of microbial diversity in poorly explored ecosystems [71]</p> <p>Advances in high-throughput sequencing: DNA metabarcoding and pipelines for analysing data [81]</p> <p>Horizon scanning [9]</p>
<b>INTRODUCTION</b>	<p><b>Prevention and surveillance, eradication</b></p> <p>Quarantine</p> <p>Monitoring/surveys</p> <p>Hygiene</p> <p>Population management/host removal</p>	<p>An IFP must be detected shortly after its introduction if eradication is to be a feasible goal</p> <p>Phylogenetically distinct species hidden within a single morphological species with a global distribution</p> <p>Morphologically identical organisms may exhibit differences in ecology</p>	<p>Fire blight eradicated in Australia [101]; pine pitch canker eradicated in France and Italy [102]</p> <p><i>Dothistroma</i> needle blight of pines, thought to be caused by one species, now known to be two species, one found worldwide, the other restricted to North-Central USA [105]</p> <p><i>Teratosphaeria</i> leaf disease of <i>Eucalyptus</i> shown to be caused by a suite of cryptic species, many with different host ranges [106]</p>	<p>High-risk site surveillance—sentinel trees near ports; sites frequented by tourists, e.g. botanical gardens [73, 82, 83]</p> <p>Multiple introductions should be avoided [69••]</p> <p>Outreach programmes/citizen science [103, 104]</p> <p>Horizon scanning, e.g. trait-based approaches/databases [66•]</p>
<b>ESTABLISHMENT</b>	<p><b>Eradication and containment</b></p> <p>Monitoring/surveys</p> <p>Hygiene</p> <p>Population management/host removal</p>	<p>Impact on host is the first sign of an invasion—often by this point already established, making eradication almost impossible</p> <p>Form novel associations with insects or other organisms, with consequent elevated pathogenicity</p> <p>Opportunities for hybridisation with resident (native or other invasive) species</p>	<p><i>Xylella fastidiosa</i> likely introduced into France years before its detection. Management challenges compounded by a diverse host range and frequent asymptomatic infection [107]</p> <p><i>Ophiostoma ulmi</i> s.l. acquired novel vectors (elm bark beetles) by replacing endemic, non-aggressive symbiont <i>O. quercus</i> [112]</p> <p>Hybrids of <i>Melampsora</i> spp. overcome resistance and cause rust on previously resistant poplar cultivars [113]</p>	<p>Measures as detailed for introduction stage</p> <p>Studies of evolutionary potential of microorganisms [69••, 70]</p> <p>Species traits that distinguish successful from unsuccessful IFPs [38, 70, 108]</p> <p>Interrogate determinates of successful eradication by studying failed and successful eradication attempts [109–111]</p>



Table 2 (continued)

Management goals and strategies	Challenges	Examples	Potential solutions/research needs
<b>SPREAD</b> Containment Control movement Hygiene Population management Disease mitigation	<p>Prediction of invasive potential based on biological and ecological traits currently poorly resolved for many IFPs</p> <p>Perception that ‘everything is everywhere’, many pathogens viewed as having a cosmopolitan distribution as result of movement of microorganisms with hosts</p> <p>Mixed reproduction strategies: sexual reproduction allows for increased genetic variation; asexual reproduction for rapid dissemination of advantageous genotypes</p> <p>Rapid evolution may facilitate spread across diverse environments and host jumps to phylogenetically divergent species</p>	<p>Extensive studies for the genus <i>Phytophthora</i> show trait-based approaches may give insights into invasion potential [114, 115]</p> <p>Population genetics study of <i>Tetratosphaeria suttonii</i> shows no geographic structure [119]. In contrast, only a single genotype of <i>T. nubilosa</i> found in north Africa and Europe [120]</p> <p>Mixed reproduction strategy of <i>Neofusicoccum parvum</i> has contributed to its successful establishment across six continents [121]</p> <p><i>Phytophthora uniformis</i>, introduced to Europe, hybridised with <i>P. x multi-formis</i>, led to emergence of aggressive <i>P. x alni</i>, cause of a devastating decline of black alder in Europe [122]</p>	<p>Identify important traits (of pathogen, host and environment) influencing invasiveness and invasibility, expand current databases [69••, 70, 108, 116]</p> <p>Tools to elucidate IFP spread across landscapes: molecular but also landscape and functional ecology [20••, 66•, 70, 117]</p> <p>Greater exploration of biological control options [26, 69••]</p> <p>Exploration of role of tree microbiota in disease regulation [69••]</p> <p>New criteria and methods for host resistance breeding [69••, 118]</p>

or a shift in the interactions with native biota. As detailed in the Unified Framework, the invasive range is determined by the extent of a suitable environment, with the environmental barrier setting the limits. Environmental filtering (where the abiotic environment prevents establishment or persistence) is an ecological concept that can be applied to the framework for IFPs, to explain why not all introduced or established species become invasive [66•]. However, the role of other mechanisms, e.g. dispersal limitation, interactions with native biota, propagule pressure, degree of host jump and microbial traits, must also be considered. After crossing the final environmental barrier across multiple sites in the introduced region, the pathogen is now fully invasive, giving rise to a disease epidemic.

### Factors influencing invasion outcomes

Burdon et al. [67•] propose an ecological-evolutionary continuum to describe host–pathogen associations, with new invasions at one end (akin to the arms-race dynamics hypothesis), and native (coevolved) associations at the other end (representing episodes of fluctuating selection). The trajectory of individual host–pathogen associations is driven by different combinations of environmental and life history attributes of host and pathogen and characteristics of the invaded community. The short- to medium-term impacts of invasive pathogens are expected to be much more visible than those of coevolved pathogens, with disease effects potentially overwhelming the host's and community's ability to respond [67•]. Over time (provided extinction does not occur), genetic and ecological changes may contribute to some degree of ecological accommodation, dampening negative impacts of the pathogen. Oak powdery mildew in Europe demonstrates this concept, changing from initial severe impact with disease epidemics resulting in tree mortality to the current equilibrium between host and pathogen and decreased disease severity

[68]. However, many other systems involving long-term interactions between IFPs and their hosts, such as chestnut blight in North America and Dutch elm disease in Europe, have not resulted in decreased pathogen virulence [68]. The long life spans of trees and their inability to adapt rapidly, where the rate of genetic change for resistance is likely to be measured in centuries [67•], increase their vulnerability to devastating disease outbreaks following the arrival of IFPs. In addition, multiple introductions of an IFP presents opportunities for intra-specific reproduction between previously isolated populations, leading to increased genetic variability and potentially increased virulence [69••].

### Management goals and strategies and the particular challenges of IFPs

One of the advantages of the Unified Framework is that it enables the mapping of management options following the stages of invasion, indicating the response efforts most likely to be relevant or successful at each stage [15••]. In Fig. 2, we identify the management goals aligned with the sequential stages of the invasion process for IFPs. Table 2 details the strategies linked to each of these management goals. As for other IASs and EIDs, control becomes more challenging and costlier as IFPs move through the stages of introduction, establishment, and spread. This is particularly the case for IFPs established in natural ecosystems, with eradication becoming virtually impossible. The management challenges, suggestions to address these, and areas of research need are summarised in Table 2. Key references are provided in Table 2, with several of these providing valuable insight into areas of research needed to address the challenges posed by IFPs [20••, 66•, 69••, 70, 71•]. Below, we provide case studies highlighting three of the major challenges encountered when managing IFPs.

### 1. *The inconspicuous nature of microorganisms*

The global trade in live plants is recognised as the pathway responsible for the greatest number of accidental introductions of invasive forest pathogens in many countries [17•, 34, 65]. Due to the sheer volume of plants in trade, just a small proportion of plants in any consignment are inspected [74, 75]. Inspections are usually limited to visual examination of aerial plant parts, therefore, asymptomatic infections or incipient symptoms limited to the roots escape detection. This may be confounded by the application of fungicides and fertilisers prior to export. Such treatments can suppress symptoms, making detection more challenging [87]. The oomycete genus *Phytophthora* is well adapted to movement by this pathway, with the movement of potted plants an important pathway for introduction, but also for spread [64], for example, *P. ramorum*, a generalist with a broad host range (> 150 spp), emerged in the USA and the UK in the mid-1990s. It quickly became widespread in the nursery trade, with long-distance dispersal traced to trade in ornamental plants [88]. The use of infested nursery stock for restoration and conservation plantings has also been highlighted as an important threat to wildlands and high conservation value areas [89]

### 2. *Cryptogenic status of many species*

Name-based biosecurity relies on robust and accepted taxonomy, but for many microorganisms, the presence of morphologically identical species and lack of information on biogeography hinders timely identification and assignment of alien status. The case study of ash dieback in Europe exemplifies these issues. First reported from Poland in the early 1990s, a biotic causal agent was not linked to dieback of European ash (*Fraxinus excelsior*) until 2006. At the time, the causal agent was identified as a novel anamorphic species, *Chalara fraxinea* [90]. In 2009, based on morphology, it was suggested this fungus was the anamorph of the ascomycete, *Hymenoscyphus albidus* [91]. This species had long been known in Europe as a saprotrophic leaf-colonising fungus, but never reported as a disease-causing agent. Only in 2011 did molecular investigations show the teleomorph of *C. fraxinea* was actually a previously undescribed cryptic species, *H. fraxineus* [92]. An Asian origin has been proposed for this species, with studies in its natural range showing *H. fraxineus* is present as an endophyte in asymptomatic leaves of *F. mandshurica* (Manchurian ash), before switching to a saprotrophic life stage during leaf senescence [93, 94]. The delay in recognising the alien origin of *H. fraxineus* precluded its inclusion in quarantine lists, and by the time its status as an IFP was fully recognised, the pathogen and resulting ash mortality had already reached many other European countries

### 3. *Rapid evolution*

Rapid evolution can occur in introduced populations as a result of selection pressures in the novel environment. This is pertinent to all taxa [95], but pathogen evolution can occur over particularly short time scales. Rapid evolution of IFPs can facilitate adaptation to novel environmental conditions and enable host jumps between phylogenetically divergent species. For example, *Cronartium ribicola*, a fungal species of Asian origin, was unintentionally introduced to the north west of the USA where it became an important pathogen causing white pine blister rust of Western white pine (*Pinus monticola*) and sugar pine (*P. lambertiana*). Genetic programs have been utilised to improve disease resistance through selection and breeding for decades; however, there has been evidence of increased pathogen virulence developing within long-term field trials [96]. Admixture, the intra-specific reproduction between previously isolated populations, and hybridization have been recognised as important mechanisms leading to the emergence of forest diseases [69••]. In particular, interspecific hybridization in the genus *Phytophthora* is increasingly observed as an important means for generating new taxa [97]. For example, *Phytophthora uniformis*, introduced to Europe, hybridised with *P. x multiformis* giving rise to the aggressive *P. x alni*, causing a devastating decline of black alder in Europe [97]

## Understanding and managing risk

The movement of plants and plant products has been repeatedly shown to be a dominant pathway for introducing IFPs [17•, 34, 65, 72]. Mechanisms exist to prevent the introduction of plant pests in the form of phytosanitary regulations promulgated through the IPPC and the WTO SPS agreement. While current regulatory efforts are having positive effects, the provisions have received criticism regarding their ability to adequately protect wildlife [9, 33, 34, 73]. In addition, the increasingly large volume and diversity of traded plants present a major challenge, with only a small percentage (estimated 2–3%) of consignments being subjected to standard inspections [74, 75]. Eschen et al. [76] developed a risk-categorisation approach (based on risk-associated information including biological characteristics and trade dynamics) to prioritise high-risk commodities. Such an approach enables the identification of commodities with elevated risk, informing priority taxa for risk assessment and directing where increased inspection resources should be allocated [76].

The lack of baseline data on microbial diversity and biogeography presents an additional challenge to existing phytosanitary mechanisms and constrains our ability to undertake pest risk analysis. For an organism to be regulated, it

must be named and known to be harmful. However, many damaging IFPs were not known to be problematic in their native range, or even known to science before they caused major damage. Linked to this is the inconspicuous nature of many microorganisms, with their ability to cause asymptomatic or latent infections precluding their detection and interception at checkpoints. The development of sensitive and rapid DNA-based detection tools enables cost-effective and high-throughput detection and quantification of pathogens with a speed and sensitivity surpassing that of traditional diagnostics [77]. These technologies represent a valuable tool for plant biosecurity. However, the use of these tools remains limited by our knowledge of organisms to be targeted. This research should be complemented by efforts to increase our knowledge of microbial diversity, especially in taxonomically rich and poorly studied ecosystems [71•]. A further challenge of DNA-based diagnostics is that DNA can persist in soil and plant tissue after death of the organism [78, 79]. This inability to distinguish between dead and viable pathogens can lead to false-positives [79]. In comparison to DNA, RNA degrades rapidly; therefore, the use of mRNA as a viability marker has been investigated as a method to overcome the risk of false-positives. While advances have been made, there are several obstacles still to be overcome before RNA-based tools can be reliably and cost-effectively deployed [78, 80]. At this point in time, traditional culture-based methods, enhanced by DNA-based molecular diagnostics, remain the most viable tools for point of entry detection and early surveillance [77, 81].

The monitoring of sentinel plants and sentinel plantings is emerging as a powerful tool for early warning and early detection of pathogen threats [73, 82, 83]. For example, the emergence of *Austropuccinia psidii* as an important pathogen of plantation eucalypts in South America provided a warning of the threat of myrtle rust to Australian Myrtaceae. Similarly, the first detection of this pathogen in South Africa was from a non-native ornamental plant, *Myrtus communis* [84]. This host is the sole representative of the Myrtaceae family in the Mediterranean Basin. Observations from South Africa indicate that *M. communis* is extremely susceptible to myrtle rust; therefore, the consequences of *A. psidii* arriving in the Mediterranean Basin will be high.

## Conclusion

The underrepresentation of IFPs in invasion science is likely a reflection of the many challenges faced in dealing with these invasions, compounded by a lack of knowledge of microbial diversity, biogeography, and ecology. Our

capacity to study microorganisms is improving rapidly, and molecular techniques, including gene and genome sequencing and metagenomics studies, have increased the “visibility” of these organisms. However, in the context of global change, forests remain vulnerable to the threat posed by the continuing arrival and establishment of IFPs. Several key focal points will enhance our ability (as a community of forest pathologists and invasion scientists) to understand and address the complex challenges of forest pathogen invasions.

There are many similarities between biological invasions and EIDs, with IFPs representing an intersection between the two phenomena. In recognition of the overlap between the aims of the IPPC and the CBD, in 2004 the secretariats of the two Conventions established a Memorandum of Cooperation to promote synergy and to avoid duplication of activities [85]. There have been ongoing efforts to strengthen this cooperation through the development and implementation of joint work plans. However, while Strategic objective B of the IPPC aims to ‘Protect the environment from the impacts of plant pests’ [86], and despite attempts to better address the objective of protecting biodiversity, the focus of phytosanitary regulations remains largely on crop pathogens. And with underrepresentation of pathogens by CBD Parties, IFPs continue to fall through the gaps. The question of how cooperation between the CBD and IPPC can best be enhanced remains pertinent. By proposing the revised framework in this review, and highlighting the challenges and areas of research need, we hope to align the work of forest pathologists more closely with that of invasion scientists, thereby addressing the urgent need for more efficient prevention and mitigation of forest pathogen invasions.

**Acknowledgements** TP and MJW acknowledge the members of the Tree Protection Cooperative Programme (TCP), South Africa, for financial support. DMR acknowledges support from the DSI-NRF Centre of Excellence for Invasion Biology and the Millennium Trust. JW thanks the South African Department of Forestry, Fisheries and the Environment (DFFE) for funding, noting that this publication does not necessarily represent the views or opinions of DFFE or its employees.

## Declaration

**Conflict of Interest** The authors declare no competing interests.

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- Of major importance

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