Approaches to Forecasting Damage by Invasive Forest Insects and Pathogens: A Cross-Assessment

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Nonnative insects and pathogens pose major threats to forest ecosystems worldwide, greatly diminishing the ecosystem services trees provide. Given the high global diversity of arthropod and microbial species, their often unknown biological features or even identities, and their ease of accidental transport, there is an urgent need to better forecast the most likely species to cause damage. Several risk assessment approaches have been proposed or implemented to guide preventative measures. However, the underlying assumptions of each approach have rarely been explicitly identified or critically evaluated. We propose that evaluating the implicit assumptions, optimal usages, and advantages and limitations of each approach could help improve their combined utility. We consider four general categories: using prior pest status in native and previously invaded regions; evaluating statistical patterns of traits and gene sequences associated with a high impact; sentinel and other plantings to expose trees to insects and pathogens in native, nonnative, or experimental settings; and laboratory assays using detached plant parts or seedlings under controlled conditions. We evaluate how and under what conditions the assumptions of each approach are best met and propose methods for integrating multiple approaches to improve our forecasting ability and prevent losses from invasive pests.

Keywords: biological invasions, forecasting models, risk analysis, screening techniques, sentinel plants

Forests worldwide are experiencing substantial and often irreversible degradation by the accidental introduction of nonnative insects and plant pathogens (Boyd et al. 2013, Brockerhoff and Liebhold 2017). This growing threat is linked to socioeconomic drivers associated with global commerce and travel that raise the likelihood of nonnative organisms traversing geographic barriers into naive ecosystems (Hulme 2009, Banks et al. 2015, Liebhold et al. 2017). Invasive insects and pathogens reduce the essential services trees provide in multiple settings ranging from wilderness areas to urban communities (figure 1; Bradshaw et al. 2016, Wingfield et al. 2017, Fei et al. 2019). The negative acute and chronic environmental impacts of nonnative pests include reduced ecosystem services, such as carbon sequestration, biodiversity, genetic diversity, hydrology, soil functions, and energy conservation (box 1) (Gandhi and Herms 2010b, Boyd et al. 2013, Freer-Smith and Webber 2017, Hauer et al. 2020, Cianciolo et al. 2021). The negative economic impacts include reduced abundance and quality of wood products, quarantine restrictions on market access, reduced residential property values, and the costs of managing established populations (Holmes et al. 2009, Aukema et al. 2011, Kenis et al. 2017). Invasive forest insects and pathogens also cause substantial cultural, aesthetic, and human health costs (Chow and Obermajer 2007, Donovan et al. 2013, Alexander et al. 2017). Additional harmful feedbacks include the increasing susceptibility of affected ecosystems to subsequent invasions by other nonnative species, increasing tree susceptibility to native insects and pathogens, and aggravating problems caused by climate and land-use change (Garnas et al. 2016, Brockerhoff and Liebhold 2017, Klooster et al. 2018).

Once they are established, high-impact invasive pests pose contentious and often irreconcilable management challenges (Blackburn et al. 2011, Lovett et al. 2016, Showalter et al. 2018, Venette and Morey 2020). A variety of response tools are available, but they all incur trade-offs and vary across systems in their efficacy, costs, environmental impacts, and human acceptance (Hurley et al. 2007, Tobin et al. 2014, Liebhold and Kean 2019). Implementing these responses can yield social inequities, such as different communities having uneven economic resources to reduce losses, and there can be particularly severe quandaries along land-use boundaries.

The underlying biological reasons why some insect and microbial species that are relatively benign, sparse, or even unknown in their native region become highly damaging in their introduced zone are complex (Eschen et al. 2015b,

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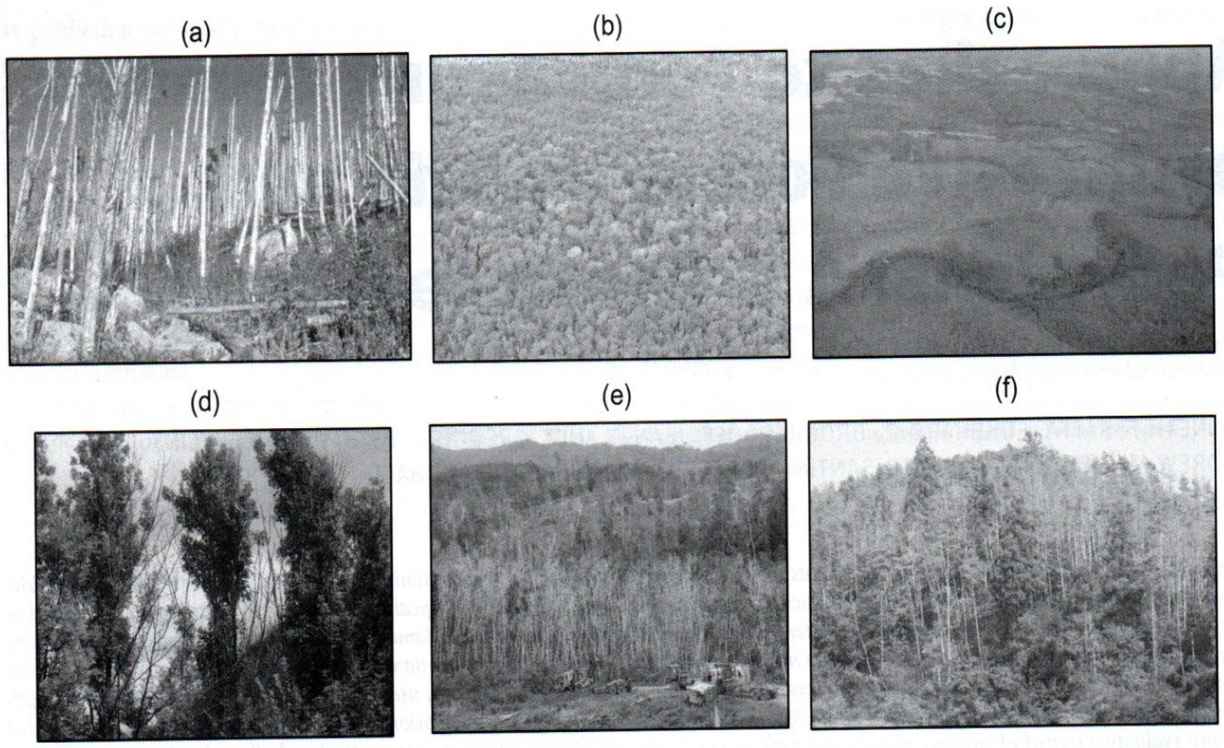

Figure 1. Examples of invasive insects and pathogens, and their impacts on forest ecosystems. Upper left: Mortality to* Abies fraseri *by* Adelges piceae *in the United States; photograph: Kenneth F. Raffa. Center: Beech bark disease in the United States; photograph: Kenneth F. Raffa. Right: Defoliation of mixed species by* Lymantria dispar *in the United States; photograph: Andrew M. Liebhold. Lower left: Ash dieback in Italy; photograph: Alberto Santini. Center:* Acacia mangium *killed by* Ceratocystis manginecans *in Indonesia; photograph: Michael J. Wingfield. Right:* Pinus thunbergii *killed by* Bursaphelenchus xylophilus *in Japan; photograph: Bernard Slippers.

Saccaggi et al. 2016, Showalter et al. 2018). However, these reasons can generally be classified into three major categories: the lack of effective natural enemies in the new region compared with a more plentiful, diverse, and adapted community of predators, parasites, pathogens, and competitors in the historical region (i.e., the loss of top-down control; Keane and Crawley 2002); the lack of evolutionary adaptation by trees in the new region compared with long-term native interactions that select for effective defenses or tolerance (i.e., the loss of bottom-up control; Gandhi and Herms 2010a); and novel insect–microbe associations formed in invaded regions in which one or both members of the complex are nonnative, resulting in increased vectoring of or infection courts for disease-causing pathogens (i.e., novel symbioses; Ghelardini et al. 2016, Wingfield et al. 2016, Paap et al. 2022).

Despite progress in our understanding of why some nonnative species escape their historical constraints to become damaging after establishing in a new region, forecasting the likelihood and extent to which individual species will become problematic before they are introduced remains highly challenging (Kolar and Lodge 2001, Kumschick et al. 2015, Mech et al. 2019). Most nonnative species either fail to establish following transport to a new region or exert little to no known impacts if they do (Williamson and Fitter 1996)—hence the ability to make such predictions is crucial for national biosecurity programs (Hulme 2011). The Agreement on the Application of Sanitary and Phytosanitary Measures of the World Trade Organization (WTO 2002) specified that to prevent protectionist policies, national governments must provide scientific evidence of risk to justify prohibitions on imports of commodities from specific countries or regions. Therefore, national plant protection organizations perform risk analyses that identify individual species that may arrive with commodities from particular countries and then evaluate the likelihoods of their establishment and impacts (Burgman et al. 2014). Better predictive capabilities would also guide more focused implementation of preshipment treatments and inspections (Sequeira and Griffin 2014, IPPC 2019a, 2019b) and postborder biosecurity (MacLeod 2015, Venette et al. 2021) while avoiding unnecessary restrictions on trade. Most countries prioritize pest species, commodities on which those pests might arrive, and countries from which those pests might originate, and these designations are based on estimates of high impacts (Saccaggi et al. 2016). Given the practical limitations, border inspections cannot directly exclude most nonnative species, but information gained from inspection on the incidence of pests and their pathways can inform decisions such as quarantines or mandatory phytosanitary treatments and motivate better phytosanitary practices (Kahn 1991, Venette et al. 2002).

Identifying species that would be harmful in a new region is also critical to effective implementation of surveillance and

Box 1. Glossary of terms.

Impact: This term has a breadth of definitions that vary with factors such as study objectives, sector of concern, presence or absence of human values, and so on (Jeschke et al. 2014). We use *impact* within the context of risk assessment, where the goal is to forecast, prevent, or lessen any economic, ecological, aesthetic, health or cultural losses caused by invasive pests.

Invasive species: A nonnative species whose introduction is likely to cause or has the potential to cause economic or environmental harm to an ecosystem or harm to human health or commerce (USFS 2013).

Pathogen: a disease-producing organism or biotic agent (D'Arcy et al. 2001).

Pest: Any species, strain or biotype of plant, animal or pathogenic agent injurious to plants or plant products (IPPC 2002). Note that *pest* includes all taxonomic and functional groups. Our analysis is restricted to herbivorous arthropods and microbial pathogens that exploit trees.

eradication programs (MacLeod 2015). Given their high costs, such efforts need to be focused on the most damaging species (Baker et al. 2019). Therefore, improved prediction schemes would better target detection programs to optimize selection and deployment of traps, allocation of inspectors, and environmental sampling (Poland and Rassati 2019). Finally, improved impact assessment abilities could expedite the targeting and prioritizing of response measures to specific threats (Showalter et al. 2018). The resulting prioritization of limited resources could include the exploration and assessment of biological control agents, the preservation of native seeds and genetic screening, bioassays assessing plant tolerance, pest-targeted genomic approaches, and region-specific impact modeling.

In response to the urgent need to reduce damaging pest invasions, various approaches have been developed to forecast potential impacts of nonnative insects and microorganisms. However, the assumptions underlying each approach have rarely been explicitly identified or critically evaluated. Rather, the urgency of each new invasive species often requires resource managers to proceed directly to specific tactics and operational details. We suggest that taking a bird's eye view of each general approach and evaluating its implicit assumptions, its scope of utility, and general advantages and limitations could help better delineate the specific applicability of each strategy and also improve their complementarity. We identify four general categories of approaches, two of which are largely experience-based and analytical, and two of which are directly empirical. These broad categories include using prior pest activity in species' native and previously invaded regions (Burgman et al. 2014, Sequeira and Griffin 2014, Kumschick et al. 2015); generalized modeling of future impacts using statistical patterns of traits, habitats, and gene sequences associated with high impact (Mech et al. 2019, Hamelin and Roe 2020); sentinel plantations and botanic gardens that naturally expose nonnative trees to potential damage from local insect and pathogen species (Eschen et al. 2019, Mansfield et al. 2019, Redlich et al. 2019); and laboratory assays using detached plant parts or seedlings (also including small ramets hereafter) under experimentally controlled conditions (Eager et al. 2004, Newhouse et al. 2014, Lynch et al. 2016). We briefly describe each approach, identify its underlying assumptions, summarize its major advantages and limitations, and evaluate how and under what conditions it best contributes to the overall challenge of predicting impacts of invasive insects and pathogens on trees. We further propose opportunities for integration, complementarity, and synergism among these approaches.

Empirical assessment of prior pest activity

Currently, the most widely applied basis for predicting impacts is prior pest activity—that is, empirical accounts of species causing damage to trees in the wild. These accounts often include descriptions of a pest's morphology, genetics, abundance, geographic distribution, host range, host symptoms, damage extent, and other factors that may affect its impacts. *Primary damage* typically refers to host mortality, growth loss, decreased reproduction, a loss of aesthetics, or altered physiology (Aukema et al. 2010, Aukema et al. 2011, Dietze and Matthes 2014, Lovett et al. 2016). *Secondary damage* includes an affected host's reduced ability to withstand subsequent biotic or abiotic stressors. These primary and secondary effects may amplify to the ecosystem level and alter species composition, biodiversity, fire dynamics, nutrient cycling, carbon sequestration, water provisioning or other processes (Kenis et al. 2009, Ramsfield et al. 2016, Freer-Smith and Webber 2017).

A major rationale for forecasting threats based on a species' impacts in its native or other invaded regions lies with international phytosanitary agreements (NRC 2000, IPPC 2019a). Specifically, the Agreement on the Application of Sanitary and Phytosanitary Measures specified that import prohibitions directed at excluding species with no prior history of causing damage are considered nontariff barriers to trade and are therefore disallowed (WTO 2002). The underlying assumption behind cataloguing particular species is that species that have exerted damage either in their native or previously invaded ranges are those most likely to cause damage if introduced elsewhere. The corollary is that species that have not caused previous damage are either unlikely to do so or the harm they would exert is less than the harm to commerce caused by attempts to exclude them.

When considering pest status, it is useful to specify whether prior impacts are primarily associated with an organism's native region or previously invaded regions (table 1). For example, prior damaging activity in regions

Table 1. Examples relating pest status of insects and pathogens in native versus introduced regions.

Status where native	Status where nonnative	Example	Primary reason for pest status in nonnative range	Selected references
Innocuous or only rarely damaging on native trees	Pest	*Dendroctonus valens*	New association with pathogen? Climatic stress to hosts? Host shift? Can sometimes be pest in native range during severe drought	Sun and colleagues (2013)
		Xyleborus glabratus	New host–fungus association with *Raffaelea lauricola*	Showalter and colleagues (2018)
		Euwallacea fornicatus sensu lato	New host–fungus association with *Fusarium* sp.	Hulcr and colleagues (2017)
		Pityophthorus juglandis	New host–fungus association with *Geosmithia morbida*	Rugman-Jones and colleagues (2015)
		Sirex noctilio + *Amylostereum areolatum*[a]	Susceptibility on naive hosts, a lack of natural enemies, and climatic stress to hosts	Slippers and colleagues (2012), Ayres and colleagues (2014), Lombardero and colleagues (2016)
		Hymenoscyphus fraxineus	Susceptibility of naive hosts	Gross and colleagues (2014)
		Xylotrechus chinensis	?	Bragard and colleagues (2021)
		Agrilus planipennis[b]	Susceptibility of naive hosts	Villari and colleagues (2016)
		Cronartium ribicola	Susceptibility of naive hosts	Showalter and colleagues (2018)
		Anoplophora glabripennis[b]	Susceptibility of naive hosts	Morewood and colleagues (2004)
		Bursaphelenchus xylophilus	Susceptibility of naive hosts	Futai (2013)
		Adelges piceae	Susceptibility of naive hosts?	Hollingsworth and Hain (1992)
		Cryphonectria parasitica	Susceptibility of naive hosts	Rigling and Prospero (2018)
		Adelges tsugae	A lack of natural enemies, susceptibility of naive hosts	McClure (1995), Montgomery and colleagues (2009)
		Ophiognomonia clavigignenti-juglandacearum	Susceptibility of naive hosts?	Furnier and colleagues (1999), LaBonte and colleagues (2015)
		Thrips calcaratus	Altered phenological synchrony?	Werner and colleagues (2006)
		Bretziella fagacearum	Susceptibility of naive hosts, new vector association	Engelbrecht and colleagues (2004)
		Ceratocystis platani	Susceptibility of naive hosts	Tsopelas and colleagues (2017)
		Profenusa thomsoni	A lack of natural enemies	Andersen and colleagues (2021)
		Dryocosmus kuriphilus	?	Rieske (2007)
		Scolytus multstriatus[c]	New fungus vector association and fungus–host association with *Ophiostoma ulmi and O. novo-ulmi*	Smith and Hulcr (2015), Santini and Battisti (2019)
Pest	Pest	*Lymantria dispar*[d]	Eruptive species, a lack of natural enemies	Liebhold and colleagues (2000)
		Hyphantria cunea[d]	A lack of natural enemies	Yang and colleagues (2015)
		Hypothenemus hampei	Multiple causes	Vega and colleagues (2015)
		Cydalima perspectalis	?	Wan and colleagues (2014)
		Cryptococcus fagisuga	Novel fungus–host association (indirect)	Cale and colleagues (2017)
		Phytophthora ramorum	Susceptibility of naive hosts	Rizzo and Garbelotto (2003)
		Phytophthora cinamomi	?	Shearer and colleagues (2007)
Innocuous	Innocuous[e]	*Hypothenemus eruditus*[f]	Secondary and extremely polyphagous (attacks 65 families of host plants)	Kambestad and colleagues (2017)
		Hylastes ater[g]	Secondary on pine roots, base of stems and stems in ground contact (quarantine pest), vector of sapstain fungi, maturation feeding on pine seedlings.	McCarthy and colleagues (2013), Sopow and colleagues (2015)
		Hylurgus ligniperda[h]	Secondary on pine roots, base of stems and stems in ground contact (quarantine pest), vector of sapstain fungi	McCarthy and colleagues (2013)

Note: The list is not exhaustive.
[a]Repeated pest impacts when introduced to multiple regions (e.g., Australia, New Zealand, South America, South Africa), primarily in *Pinus radiata* (native to western United States) plantations. No significant impacts in eastern North America *Pinus* spp., where primary host, *P. radiata*, is absent.
[b]Primarily associated with dead or severely stressed native trees in China, but attacks live North American tree species planted there.
[c]Not a pest in Europe until *O. ulmi* introduced to there from China; it was introduced as a complex to North America.
[d]More severe pest in introduced than native range.
[e]Although we give only three examples, most insect and perhaps fungal establishments fall within this category. Potential displacement effects on native species are not typically estimated when assigning pest status.
[f]Colonized 37 landmasses, among which Europe, North, Central and South America, Africa, Asia, Australia.
[g]Europe, Australia, New Zealand, South America, Asia.
[h]Europe, Australia, New Zealand, North America, South America, Asia.

that an organism has previously invaded can be an informative, although imperfect, indicator of future pest status (Causton et al. 2006, Lodge et al. 2006, Okabe et al. 2012, Fournier et al. 2019). This information can also help provide guidance to other approaches, such as choosing tree species for *ex patria* sentinel plantings and choosing candidate insects and pathogens for screening.

Species with documented damage in invaded regions. Species that became problematic in invaded ranges appear to be of particular concern for causing future harm if introduced elsewhere (NRC 2002, Kumschick and Richardson 2013). For example, 95% of damaging nonnative forest insects and pathogens in Australia were damaging in other parts of the world (Nahrung and Carnegie 2020). An example is *Sirex noctilio*, which has caused substantial impacts in multiple continents (table 1). A species that is problematic only in its nonnative range has likely encountered naive hosts with inadequate defenses (Gandhi and Herms 2010a), or escaped the suppressive effects of natural enemies (Jeffries and Lawton 1984).

Species with documented damage in native regions. Some insects and pathogens undergo periodic outbreaks within their native geographic range because they evolved mechanisms to overcome some host defenses or respond quickly to intermittent disruption of ecological constraints. For example, the defoliator *Lymantria dispar* is native to Europe, Asia, and portions of North Africa, where outbreaks sometimes occur in addition to the even greater damage it causes in its nonnative range in the United States (Giese and Schneider 1979, Johnson et al. 2005). Therefore, *L. dispar* is the target of focused biosecurity activities in many countries and regions. In other cases, species that are major pests in their native range have not proven to be adept invaders. For example, *Ips typographus* is the most harmful European forest pest, and is likewise one of the most frequently detected bark beetles in imported goods worldwide. But these introductions have never resulted in establishment (Brockerhoff et al. 2006b, Turner et al. 2021). The Precautionary Principle dictates, however, that this domestically highly damaging species remains on quarantine lists at least until further research fully clarifies the reasons for its failure to establish.

Species without prior documented damage. Differing viewpoints remain about species that have never been reported as pests. One position holds that if a native insect or pathogen is strongly regulated by natural enemies or coevolved defenses, it would not reach pest densities until it is released from these forces. From this perspective, any species could become a pest if it were introduced in a new area where these forces are absent and other biotic and abiotic requirements are met. The ample number of such species in table 1 lends support to this view. Consequently, some have argued that any nonnative species could be capable of causing harm once introduced (i.e., guilty until proven innocent; e.g., Mack et al. 2000, Campbell 2001). A second, related viewpoint maintains that the absence of evidence for the impacts of a species should not be construed as proof it has no impact. For example, damage to healthy trees may be so slight that it is overlooked, or described only in local, largely inaccessible sources until after the species became highly damaging elsewhere (Rizzo and Garbelotto 2003, Wei et al. 2004, Crystal-Ornelas and Lockwood 2020). This lack of information is particularly acute for plant pathogens; the majority of global fungi are undescribed and many introduced pathogens are relatively innocuous in their native ranges (Eschen et al. 2015b). Even among insects an estimated 80% of species remain undescribed (Stork 2018). A third perspective maintains that a nonnative species should not be considered a risk until harm is demonstrated (i.e., innocent until proven guilty). Without empirical evidence, any projection of future damage is considered too speculative and uncertain. For example, an estimated 86% of nonnative forest insects established in the United States have not generated reports of damage there (Aukema et al. 2010). Therefore, it is both true that most nonnative insects and microbes do not exert noticeable damage, and that many or perhaps most damaging nonnative insects and microbes were not highly problematic prior to being moved from their native range. Hence the quandary.

Ecological impacts attributed to catalogued invasive species. In addition to highlighting species of particular concern, observations on prior pest activity can provide valuable information for augmenting the other general approaches. That is, accompanying life history and phylogenetic records provide the raw data for developing predictive models and guiding sentinel plantings and bioassays relating to specified insect and microbial taxa.

Host range typically shows strong phylogenetic relationships. Therefore, pests reported from only one host species are at least initially presumed unlikely to affect others, those recorded on multiple species or genera are considered likely to affect other members of the family, and those on multiple host families are deemed likely to affect multiple species not yet encountered. Insects and pathogens show substantial variation in their performance on different species within their host range, but unfortunately the extent of variation is usually unknown prior to invasion. There can also be high intraspecific variation in host susceptibility (Bus et al. 2008, Giampetruzzi et al. 2016). Adding to the complexity, some pathogens rely on several different host species to complete their life cycle, and some wood-boring insects, symbionts, and opportunistic fungi are primarily limited to physiologically stressed hosts in their native range but exhibit less of this constraint in their introduced range (Slippers and Wingfield 2007, Akbulut and Stamps 2012, Wermelinger and Thomsen 2012, Futai 2013, Hulcr et al. 2017, Marsberg et al. 2017).

Climatic suitability describes the potential for populations to persist and grow under various temperature and moisture regimes. Climatic conditions under which a pest has been reported can be used to describe its climate envelope,

with occurrence reports used to distinguish between well established and ephemeral populations. Impacts are more likely in new areas that are climatically similar to previously affected sites (Venette 2017, Canelles et al. 2021).

Insect–microbe associations are particularly threatening, but the nature of these associations varies widely. For example, all insects harbor symbionts that contribute multiple functions (Douglas 2015), but when introduced into novel plants some symbionts cause widespread damage. Examples include mortality to over 300 million *Persea borbonia* by *Xyleborus glabratus* and its symbiont *Harringtonia (Raffaelea) lauricola* in North America (Hughes et al. 2017, de Beer et al. 2022) and chronic losses to the highly invasive woodwasp *S. noctilio* and its symbiont *Amylostereum areolatum,* worldwide (Slippers et al. 2012). Other novel associations in colonized areas include *Monochamus* spp. (Cerambycidae) vectors of *Bursaphelenchus xylophilus.* North American pines generally tolerate infection by this native nematode but following introductions into Japan, China, Korea, and the Iberian Peninsula it became associated with local *Monochamus* species and killed numerous susceptible indigenous pine species (EPPO 2022). Some disease epidemics result from replacement of a nonaggressive native microorganism in an existing association with a nonnative pathogen, as with Dutch elm disease (*Ophiostoma ulmi* s.l.-*Scolytus* spp.; Santini and Battisti 2019). Independent co-occurrence of an otherwise harmless fungus and harmless insect can also have major consequences. For example, in its native Europe and Caucus Mountains, *Cryptococcus fagisuga* feeds on the bark of native *Fagus sylvatica* and any resulting entry by the fungus *Nectria coccinea* is usually tolerated. However, when *C. fagisuga* was introduced into North America, it colonized American beech (*Fagus grandifolia*) and allowed entry by local fungi, *Neonectria faginata* and *Neonectria ditissima.* On this naive highly susceptible host, this new insect–fungus association has caused high mortality (Houston 1994, Cale et al. 2017). Nonnative insect–microbe complexes pose special challenges to ascribing impacts and therefore making regulatory decisions. For example, *B. xylophilus* and its nonnative *Monochamus* spp. Vectors are both listed as quarantine organisms by the European Union and United States (EU 2019, APHIS 2022, EPPO 2022), although it is typically native *Monochamus* that acquire this invasive pathogen. In other associations, regulations are directed at the vector. For example, *S. noctilio* but not *A. areolatum* is on the US quarantine list (APHIS 2022) and the EU lists non-European Scolytidae but not their fungal associates as quarantine organisms (EU 2019).

The availability of effective management strategies can influence a pest's impact ranking. The ease and accuracy with which a species can be detected and delimited is critical, and depends on whether it responds to long distance attractants such as pheromones or plant volatiles (Tobin et al. 2014, Fan et al. 2019). Such rapid detection and delimitation opportunities arise more frequently with insects than pathogens. However, pathogens that rely on insect transport can sometimes be sampled indirectly by attracting and trapping the vector (Moore et al. 2019, Smallwood et al. 2022). The efficacy of silvicultural practices, tree resistance, and natural enemies can also be quantitatively assessed in the areas of origin to help evaluate risk and guide postinvasion responses. For example, releasing *Rhizophagus grandis* (Monotomidae) provided complete control of *Dendroctonus micans* in France, the Republic of Georgia, Britain, and Turkey (Grégoire 1988, EFSA 2017), and, biological control agents combined with thinning was effective against *S. noctilio* in New Zealand, but less so in South America and South Africa (Hurley et al. 2007, Slippers et al. 2012).

Advantages and limitations of species watchlists. Identifying prior damage by particular species is the only approach currently widely used to set biosecurity policies. It also more readily lends itself to immediate cataloguing, is most readily communicated, and is the most directly based on specific experience. Cataloguing prior impacts can be complicated by the diversity of impacts studied, the spatiotemporal scale at which impacts were quantified, and the methods used to classify damage (Aukema et al. 2011, Mech et al. 2019, Crystal-Ornelas and Lockwood 2020, Schulz et al. 2020). Insects and pathogens that have demonstrably caused damage in invaded regions merit special attention, and information about their physiognomy, host range, climatic envelope, symbioses and management potential can further delineate risk. Species that are known pests in their native region also merit attention and include examples both where they did or did not become highly problematic in new regions. Watch lists are less effective at identifying species that are largely benign in their native region but would become pests if transported to naive ecosystems. Unfortunately, many of our most historically damaging invasive pests arose from this category (Liebhold et al. 2012, Ayres et al. 2014, Eschen et al. 2015a, Hughes et al. 2017, Bonello et al. 2020). From an evolutionary and ecological standpoint this is not surprising, because very powerful top-down, bottom-up, and lateral forces generally constrain populations below damaging levels in coadapted systems but are often lacking or reduced in nonadapted systems (table 1). This uncertainty is a major influence driving recent shifts in emphasis from species watch lists to pathway mitigation and other "horizontal measures" (Eschen et al. 2015b, Grousset et al. 2020). However, such general approaches have their own limitations because they can be costly to implement and constrain free trade. Therefore, additional indirect and direct approaches are needed.

Predictive models based on traits of pests and hosts

One approach to contending with the sheer number of potentially damaging nonnative species is to relate information on insect, pathogen, or host traits, phylogenies, or genomes to cross-species patterns of damage to discern general trends from which to predict specific likelihoods of impact. Therefore, quantitative impact prediction systems

(i.e., models) have the potential advantage of forecasting future establishments and impacts based on particular traits or gene sequences of previously established species. Predictive models provide the most all-encompassing and logistically unconstrained of all forecasting approaches. Typically, such models consider various components of risk that include probability of transport, probability of establishment and anticipated level of damage (Burgman et al. 2014, Enders et al. 2020). Plant protection organizations can apply these models to assess potential risks associated with specific commodities, impose prohibitions on their import and determine postborder responses to newly detected incursions (Devorshak 2012, MacLeod 2015).

The overriding assumption of quantitative impact prediction systems is that patterns emerging from either prior invasions or basic biological relationships can provide reliable, general, and useful predictions of impacts arising from future invasions. The specific assumptions vary with each model depending on the attributes being examined. Models vary in the extent to which they are purely correlative and descriptive versus connected to mechanistic processes. A key advantage of this approach is that it provides very broad and widely applicable generalizations. In particular, models can address large numbers of permutations of putatively important factors, species, and interactions without the high costs, infrastructure requirements, and time delays demanded by actual experimentation. The main disadvantage is that models often generate highly variable output, which may be too general and uncertain to translate into specific practical policies. Furthermore, the low absolute number of high-impact invasions provide limited replication, so models fit to historical invasions may be sensitive to new introductions that deviate from prior relationships. In addition, some of the information needed to apply analytical models to practical forecasting may be lacking for many species in their native regions.

Several models have been developed to predict the probability of transport and establishment of potential invasive species, with varying degrees of accuracy (Eschen et al. 2014, Enders et al. 2020). For example, certain insect orders or families are more likely to be introduced and establish than others (Liebhold et al. 2016, Liebhold et al. 2021, Mally et al. 2022). In addition, specific life history traits have been found to predict probabilities of insect and to a lesser extent fungal establishment (Simberloff 1989, Suarez et al. 2005, Philibert et al. 2011). For example, some reproductive systems such as sib mating and parthenogenesis are believed to enhance establishment by low-density founding populations and have been associated with invasion success in Scolytinae (true bark beetles and ambrosia beetles) and Hemiptera, respectively (Brockerhoff and Liebhold 2017, Grousset et al. 2020, Lantschner et al. 2020, EPPO 2020a). Statistical models have also been developed to predict probabilities of insect transport and establishment based on the distribution of other invading species, volumes of imports from different regions, and specific pathways (Liebhold et al. 2012, Worner et al. 2013, MacLachlan et al. 2021), and climatic niche models can predict potential geographical ranges of specific insect invaders (Venette 2017, Koch 2021). Machine learning approaches hold future promise to refine such tools (Morey and Venette 2020).

In contrast to models that forecast transport and establishment risk, there has been relatively little work developing and applying models to predict potential impacts of insects and even less with phytopathogens. Although some systems have been developed to quantify the impacts of currently established species and apply that information to prioritize postborder biosecurity activities (Kumschick et al. 2012, Roy et al. 2018), this work cannot be readily applied to predicting damage of species that may establish in the future and prioritizing preborder biosecurity. For example, it cannot be assumed that features such as spread rates predict herbivore population outbreaks or pathogen aggressiveness (Tobin and Raffa 2022). This scarcity of research differs markedly from preestablishment impact modeling conducted with plants, which has been performed more extensively and successfully (Weber and Gut 2004, Skurka Darin et al. 2011, Kumschick and Richardson 2013). However, some fundamental differences with plants limit extrapolation to insects and pathogens. For example, interspecies trade-offs between reproductive investment versus longevity that have proven useful for forecasting plant invasion cannot easily be applied to insects or microbes. Likewise, low habitat diversity increases susceptibility to invasion by plants, but regions with high plant diversity may be more invasible to heterotrophs because they provide a higher likelihood that a suitable host species will be present (Niemelä and Mattson 1996, Liebhold et al. 2013, Guo et al. 2021, Ward et al. 2022). In contrast to establishment, the impacts of insects and pathogens tend to be lower in high-diversity habitats because of their associated population regulating features (Jactel and Brockerhoff 2007, Nunez-Mir et al. 2017).

Species traits associated with impact. In general, traits associated with individual insect species have not proven to be very predictive of their impact. Mech and colleagues (2019) evaluated a range of life history traits among 58 nonnative conifer-feeding insects that had established in North America, but did not find any of them to be associated with the magnitude of their impacts on forests. Likewise, Schulz and colleagues (2021) did not find any association between life history traits and impacts of 100 nonnative insects feeding on woody angiosperms in North America.

As with insects, relatively few studies have attempted to predict postestablishment impact of phytopathogens based on traits. Invasion success was predicted for fungal pathogens using species-level predictors such as dispersal distance, type of reproduction, spore characteristics, and some temperature characteristics for growth and parasitic specialization (Philibert et al. 2011). The production of abundant airborne spores with high dispersal potential helps explain the high representation of fungi such as powdery

(Erysiphales) and downy (Peronosporales) mildews among high-impact invasive pathogens (Desprez-Loustau et al. 2010). Root-infecting oomycete pathogens had a broader host range and were reported in more countries than their aboveground counterparts (Barwell et al. 2021), and faster growing species that produce thick-walled resting structures had broader host ranges (Barwell et al. 2021). Phenotypic plasticity can also be important by contributing to ecological fitting (Prospero and Cleary 2017). For some obligate parasites such as rust fungi (Pucciniales), traits such as heteroeciousness (requirement to alternate between distinct hosts to complete life cycle), can be a limiting factor when only one required host is present (Desprez-Loustau et al. 2010).

Understanding how fungal and insect traits may influence their potential to invade and affect forest ecosystems clearly has potential and could be incorporated into pest risk assessment. A major challenge is the paucity of databases that can be queried. For example, pathogens are largely inconspicuous despite the highly visible symptoms they often cause and are, therefore, far less represented in invasive species databases than insects or plants (Desprez-Loustau et al. 2010, Paap et al. 2020). In particular, a large fraction of nonnative fungal phytopathogens are innocuous plant associates in their native range, and most such fungal species are undescribed and largely unknown to science (Cleary et al. 2016). Because innocuous fungal species virtually never receive any attention, it is impossible to compare innocuous fungal species with those that have postinvasion impacts.

Phylogenetic predictions. Phylogenetic similarity to hosts in the native range is a primary determinant of the likelihood that a novel tree species in the invaded range will be a suitable host for a given nonnative insect or pathogen (Bertheau et al. 2010). A model by Pearse and Altermatt (2013) successfully predicted the use of hosts by nonnative Lepidoptera on the basis of phylogenetic similarity to native hosts. Similarly, the likelihood that a pathogen can infect two plant species decreases with phylogenetic distance between them (Gilbert and Webb 2007). Although such results are promising there are some caveats. Predicting infection potential of pathogens by phylogenetic distance of hosts was evident for foliar ascomycetes (Gilbert and Webb 2007), but would not apply to basidiomycete and oomycete pathogens with broad host ranges such as *Armillaria ostoyae* and *Phytophthora ramorum*. Phylogenetic similarity of trees within versus between the northern and southern hemispheres provides support for the supposition that there is a greater chance of pests invading within versus between hemispheres. Examples include the stem canker pathogens in the Cryphonectriaceae. The best known of these is the chestnut blight pathogen *Cryphonectria parasitica*, but other *Cryphonectria* spp. also infect various Fagaceae across the northern hemisphere (Gryzenhout et al. 2006). In contrast, species of *Chrysoporthe* (and some other genera) also members of the Cryphonectriaceae are important pathogens of the Myrtales, including Myrtaceae (e.g., Eucalyptus) and the Melastomataceae (e.g., *Tibouchina*) across the southern hemisphere (Gryzenhout et al. 2006). An implicit assumption of models based on host phylogenetic relationships is that these phylogenies are well understood, although, in practice, many undergo continual revision. Alleviating this concern somewhat are recent results showing that some emergent predictions can be relatively robust to differing, recent plant phylogenetic models (Uden et al. 2022).

Within the broad category of phylogenetic relatedness, other factors, such as feeding guild, can add predictive power. Mech and colleagues (2019) found that the impacts of nonnative folivores of confers were greatest on the host conifers that are most closely related to the invaders' native tree species, but, among sap feeders, the impacts were greatest on hosts of intermediate phylogenetic similarity. That is, the damage was reduced on nonnative hosts that were either too closely or too distantly related to the native hosts relative to a phylogenetic zone of greater susceptibility. Similar results of intermediate phylogenetic similarity were found in an analysis of invasions by insects feeding on woody angiosperms in North America (Schulz et al. 2021). Mech and colleagues (2019) in addition, found that conifer-feeding insects were more likely to have high impacts when the new host lacked a congeneric native insect herbivore. These findings stress the potential importance of both host associations with insects and pathogens and phylogenetic relationships between native and nonnative hosts for predicting the impacts of introduced pests. This type of information could be assembled in future statistical models to predict the impacts of insect species that have not yet been introduced and be applied in biosecurity risk assessments.

Models have also been used to evaluate phylogenetic relationships among potential invaders, with mixed results. For example, Grégoire and colleagues (2023) identified several drivers that are widespread among invasive, damaging bark and ambrosia beetle species, but none of these traits were shared by entire taxa. From a management perspective however, phylogenetic relatedness of an invader to known native species can facilitate identifying traits such as pheromone chemistry, symbionts, and natural enemy complexes.

Genomic analyses. Genome analyses potentially offer a new approach to predicting traits associated with the impacts of invasive insects and pathogens. To date, this idea has been pursued more aggressively with pathogens. There are two general approaches. The first compares genomes of different species to identify the determinants associated with certain traits or lifestyles. For example, fungi are highly diverse and function as symbionts, saprobes, and pathogens. The probability of being a pathogen or saprobe could be predicted with high accuracy by comparing the genomes of the Dothideomycetes, a large fungal family that includes several tree pathogens but also some saprobes (Haridas et al. 2020). Genome sequencing of members of the genus *Cryphonectria*, which includes both nonpathogenic species

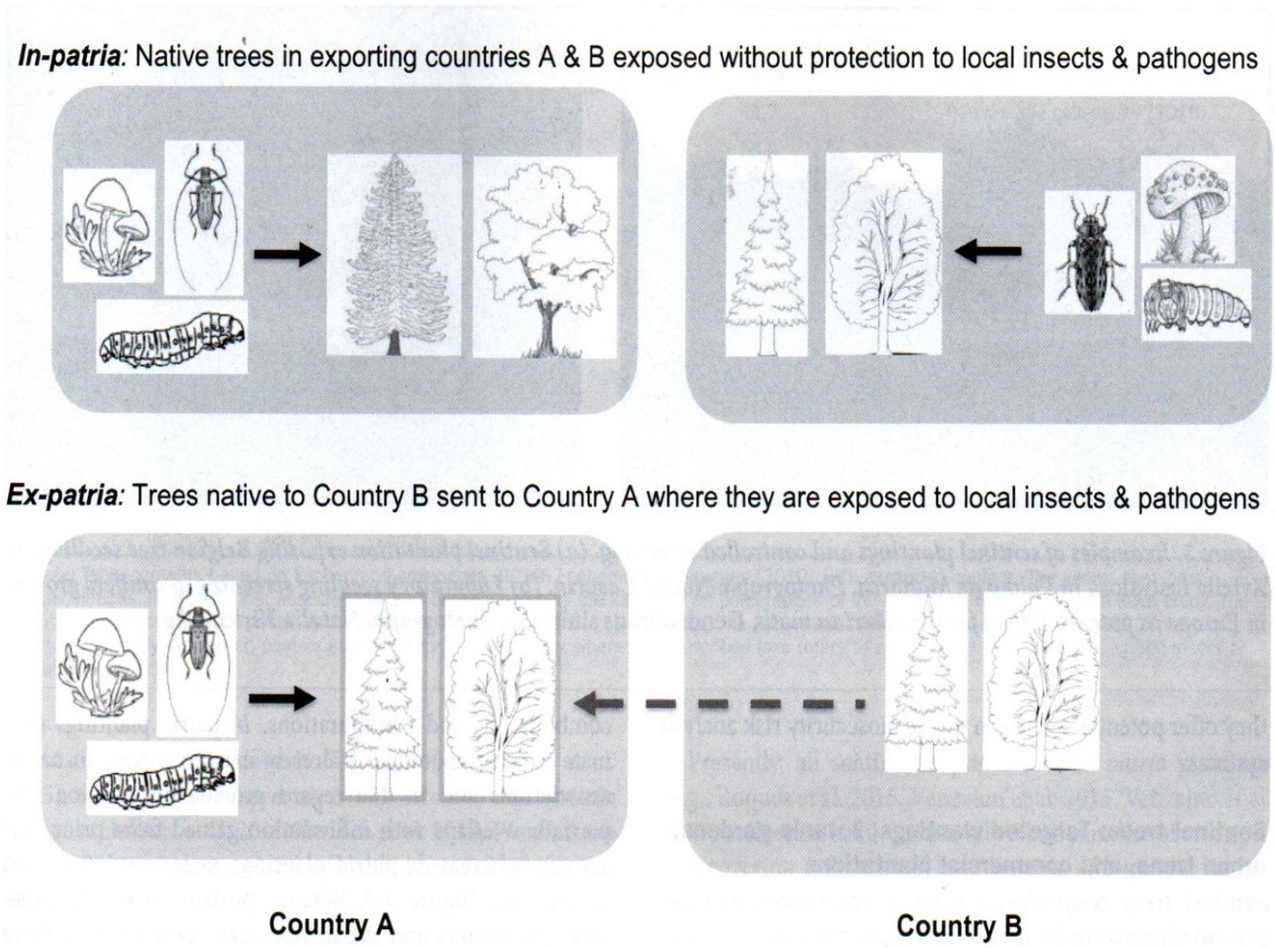

Figure 2. Diagram of sentinel plantings used to help forecast damage by nonnative pests. **In patria** ***sentinels are native trees in an exporting country left exposed to native insects and pathogens. The intent is to detect problematic hitchhikers before transport to a new region. Such plantings can be strategically located near shipping hubs and are also called*** **sentinel nurseries. Ex patria** ***plantings involve sending trees from an importing country to an exporting country. These are also called*** **sentinel plantations,** ***and the transfer of trees may be unidirectional, reciprocal, or networked. A third category of planted trees that can be used as sentinels includes existing trees in botanic gardens, arboreta, large-scale plantations, and urban settings (parks, amenity gardens, roads). These can include both native and nonnative species in various combinations and configurations.***

and *C. parasitica*, revealed a genomic pattern associated with the transition to pathogenicity from a nonpathogenic ancestor and could therefore be used to predict pathogenicity (Stauber et al. 2020). A second approach uses genomic variation within a species to identify markers associated with traits. A genome-wide association study was used, for example, to predict virulence in the pathogen *Heterobasidion annosum* (Dalman et al. 2013). Genome sequencing of a worldwide collection of the pathogens that cause the Dutch elm disease revealed that some genome regions originated from hybridization between fungal species and contained genes involved in host–pathogen interactions and reproduction (Hessenauer et al. 2020). This could have generated genomic innovations that allowed the pathogen to spread and infect its host, because isolates with hybrid genomic features had enhanced growth rate and pathogenicity in an *in vivo* model. These few examples highlight the potential of genomics to help predict traits that are relevant to insect and disease epidemics. As molecular databases increase in size, genomic approaches could be refined to reveal signatures associated with additional invasiveness and impact traits, such as sporulation, sexual reproduction, and host specificity.

Advantages and limitations of general predictive models. Models based on traits, phylogeny, and genomics offer potential for rapid and inexpensive prediction of pest damage. Although these methods are limited by the need for an a priori list of candidate pest species and detailed information about each, as well as considerable inherent uncertainty, they offer the possibility of exploring large numbers or species and could therefore be used as a first pass to highlight those potentially dangerous species that merit further attention. These prediction methods are still early in their development, but

Figure 3. Examples of sentinel plantings and controlled screening. (a) Sentinel plantation exposing Belgian tree seedlings to* Xylella fastidiosa *in Palma de Mallorca. Photograph: Noemi Casarin. (b) Laboratory seedling screening of conifers grown in Europe as potential hosts for the Siberian moth,* Dendrolimus sibiricus. *Photograph: Natalia Kirichenko.

they offer potential for use in future biosecurity risk analysis systems.

Sentinel trees: Targeted plantings, botanic gardens, urban trees, and commercial plantations

Sentinel trees encompass a suite of approaches that can potentially provide the most direct tests of tree susceptibility and the putative impact of species that might be moved by international trade. The sentinel plant strategy was progressively developed and refined to help address the problem of major damage often being caused by species about which little if anything was known prior to invasions (NRC 2002, Britton et al. 2010, Barham et al. 2015, Roques et al. 2015, Vettraino et al. 2015, Eschen et al. 2019, EPPO 2020b). The International Plant Sentinel Network was founded to coordinate international efforts, facilitate information exchange, and support sentinel plant research within botanic gardens and arboreta (Barham et al. 2015). Several methods of using sentinel plants follow this initial or expanded protocols (figure 2).

Three main types of sentinel plants have been defined (Barham et al. 2015, Eschen et al. 2019, Morales-Rodriguez et al. 2019, EPPO 2020b): *in patria* plantings (or sentinel nurseries) consist of plants native to the exporting country that are surveyed for pests that may enter a pathway of introduction to the importing country; *ex patria* plantings (or sentinel plantings) consist of plants native to the importing country that are planted in the exporting country and surveyed to identify damage that might occur if local insect herbivores and microbial pathogens were accidentally introduced to the importing country; and existing plants in botanic gardens, arboreta, large-scale plantations and urban settings (parks, amenity gardens, roads) that can include both native and nonnative plant species in various combinations and configurations. *In patria* plantings estimate infestation rates of already existing native-to-native associations and in that regard provide information that partially overlaps with information gained from prior pest activity, whereas *ex patria* plantings assess new pest–host associations (figure 3a). Botanic gardens, arboreta, large-scale plantations and urban trees can serve both of these purposes, depending on circumstances.

The three approaches offer different types of information useful for pest risk assessment (*ex patria* plantings), commodity risk assessment (*in patria* plantings), or studying host-shift events and novel pest–host associations (botanic gardens, etc.; Morales-Rodriguez et al. 2019). Sampling designs, diagnostic procedures, and detection tools may vary according to the scope and the objectives of research and operational projects. In *ex patria* plantings, large-scale plantations, and urban trees, the causal agent of an infection or infestation has to be identified, whereas, in sentinel nurseries, all the taxa associated with the sentinel species are identified to ascertain whether they can become a threat to plants in the new ecosystem (Morales-Rodriguez et al. 2019). Examples of the sentinel plant method are given in table 2, which shows substantial success at detecting new, previously unknown plant–host associations, as well as entirely unknown taxa found on the studied sentinel plants. The value of using plants near hubs of human-mediated transport to detect and assess accidentally introduced organisms is gaining increased acceptance (Eschen et al. 2019, Morales-Rodriguez et al. 2019). Locating pests in urban areas can also facilitate eradication efforts. Most introductions of nonnative forest insects are first detected in urban areas where imports arrive (Branco et al. 2019), whereas pathogen introductions are more commonly detected in forests (Santini et al. 2013). The locations of interest include

Table 2. Results of sentinel plant studies conducted in various countries to detect new pest–host associations.

Planting type	Target pests	Location	Type	Associations				Reference
				Known	New	Undescribed taxa	Total	
Ex patria	Insects	China	Plantation	3.1	54.2	42.7	104	Roques and colleagues (2015)
Ex patria	Pathogens	China	Plantation	0.5	20.9	78.6	182	Vettraino and colleagues (2015)
In patria	Insects	China	Plantation	31.6	25.2	43.2	220	Kenis and colleagues (2018)
In patria	Pathogens	China	Plantation	0.0	17.0	83.0	106	Vettraino and colleagues (2017)
Ex patria	Insects	Russia	Botanical gardens	83.6	16.4	0.0	146	Kirichenko and Kenis (2016)
Ex patria	Pathogens	Russia	Botanical gardens	56.7	43.3	0.0	67	Tomoshevich and colleagues (2013)
Ex patria	Insects Pathogens	South Africa	Botanical gardens	0.0	100.0	0.0	2	Paap and colleagues (2018)
Ex patria	Pathogens	South Africa	Botanical gardens	75.0	0.0	25.0	12	Hulbert and colleagues (2019)
Ex patria	Insects (aphids)	New Zealand	Botanical gardens	62.9	37.1	0.0	35	Redlich and colleagues (2019)

Note: Table contents based on Eschen and colleagues (2019) Eschen and colleagues (2019), with expanded content. The *known* pest–host associations, *new* pest–host associations, and *undescribed taxa* are indicated as percentages of the total of all recorded taxa in each study. The total number of detected pest–host relationships in each study is also indicated. The *known* and *new* pest–host associations refer to previously known or newly discovered pest–host associations, respectively, whereas *undescribed taxa* refers to associations involving undescribed insect or pathogen species.

ports and airports (Brockerhoff et al. 2006a, Rassati et al. 2015), urban areas (Paap et al. 2017), arboreta and botanic gardens (Hulbert et al. 2019, Redlich et al. 2019, Wondafrash et al. 2021), and plant nurseries (Liebhold et al. 2012, Santini et al. 2013).

The assumptions underlying sentinel plantings vary with each approach, but in all cases, their reliability hinges on adequate sample sizes and distributions of test trees to effectively assess local fauna and flora across the needed range of environmental variance, and that a statistically reliable estimate of requisite sample size can be calculated. Second, there is an assumption that trees planted outside their native range (*ex patria* plantings, botanic gardens) or typical habitat (*in patria* urban, garden, plantation) are accurate surrogates for the same species in its native conditions, despite their different trophic relationships (e.g., mycorrhizae, endophytes, predisposing agents such as root pathogens, defoliators, and mistletoes), soil conditions, and so on.

Advantages and limitations of sentinel plants. The sentinel plant method, as inclusively defined in the present article, can be considered the most direct approach to detecting and identifying potential threats to woody plants native to particular regions and also the most specifically proactive, because it can reveal threats that are not yet known. This allows the importing country to be prepared for and possibly regulate imports to reduce the likelihood of arrival of new threats by performing an appropriate pest or commodity risk assessment and implementing tools to prevent their introduction and establishment (https://https://dx.doi.org/10.32942/osf.io/k9jdy [preprint: not peer reviewed]). Each sentinel strategy has its own underlying assumptions, advantages, and limitations as summarized in tables 3a and 3b and discussed below.

Presently, all sentinel *in patria* and *ex patria* plantings (e.g., Roques et al. 2015, Vettraino et al. 2015, Vettraino et al. 2017) are restricted to a relatively small number of tree species covering only a small area because of logistical limitations. However, they can be extended to more species of both economic and ecological importance, over larger areas, and with sufficient replication for each species to allow statistically sound experiments. The area and replication needed to detect all relevant threats is difficult to calculate. In general, the area over which nonnative trees are planted increases the number of insect species recruited (Branco et al. 2015). Even when these conditions cannot fully be met, *in patria* and *ex patria* plantings can provide new knowledge about host associations that are currently poorly understood and this knowledge can inform both detection and modeling efforts.

In patria and *ex patria* plantings also pose some challenges. For example, it is important to find matching environments that fully encompass the range of relevant climatic and ecological characteristics in potential source regions (Eschen et al. 2019), which is often difficult. Furthermore, the macro and micro environments of each planting must be suitable for potential vectors of phytopathogens, and also provide appropriate secondary hosts where required for pathogen or insect development. Regardless of the sentinel plant method applied, the sampling intensity has to be assessed for each location, and the costs of surveys, sampling and identification can be very high. Another logistical challenge is that many insects and pathogens show strong associations with particular tree age categories such as maturity or older, so there can be substantial delays until comprehensive data can be obtained from new sentinel plantings. This challenge is more problematic for some groups, such as wood-boring insects or stem canker fungi than others. Also, a high density

Table 3a. Relative contributions of the various types of the sentinel plant method.

Contribution	Sentinel plantings *ex patria* plantings	Sentinel nurseries *in patria* plantings	Botanic Gardens and arboreta	Large-scale plantations	Urban trees
Ability to identify possible new pest–host associations	√		√	√	√
Potential to plant an adequate number of trees per species	√	√		√	
Potential to plant many species	√	√	√		√
Potential to plant multiple genotypes	√	√			(√)
Ability to implement robust experimental planting designs	√	√		(√)	
Pest risk assessment	√	√	√	√	
Commodity risk assessment		√			
Low cost of establishment		√	√	√	√
Low cost of maintenance		√	√	√	√
Young trees (seedlings, plantlets, saplings)	√	√	√	√	(√)
Mature trees			√	√	√
Records of previous attacks may be available			√	√	
Many individuals, large area covered, and longer time since planting				√	
Many individuals grown in homogeneous stressing conditions					√

Note: Some rankings are in parentheses because the condition can be fulfilled in theory but is often not fulfilled in practice.

Table 3b. Relative limitations of the various types of the sentinel plant method.

Limitation	Sentinel plantings *ex patria* plantings	Sentinel nurseries *in patria* plantings	Botanic Gardens and arboreta	Large-scale plantations	Urban trees
Legislative difficulties in setting up (Vettraino et al. 2020)	√				
Logistic constraints (e.g., planting, watering, fencing, surveillance)	√	√			
Number of plant species typically limited	√			√	
Reduced number of pests detectable because of young trees	√	√		√	
Biased number of pests detectable because of old trees			√	√	√
Limited number of possible challenged provenances within species			√	√	√
Sampling intensity to be assessed	√	√			
High costs of survey and identification	√	√		(√)	√
Relatively small number of all possible environmental conditions under which challenges to insects and pathogens occur	√	√			
Narrow genetic base			√	√	√
Grown in stressing conditions					√
Deals solely with bottom-up trophic interactions: Cannot predict impacts that would arise from reduced top-down forces or new insect–microbe associations that might occur in invaded region.	√	√			

Note: Some rankings are in parentheses because the condition can be fulfilled in theory but is often not fulfilled in practice.

of test plants may be needed not just for statistical replication but also to generate sufficient population pressure. Densities of many pests follow the resource concentration hypothesis, under which population growth is closely tied to the density and spatial extent of hosts (Root 1973). Consequently, the potential for pests to reach damaging levels may only be expressed if hosts are planted in pure stands over large areas (Damien et al. 2016). In the case of *ex patria* plantations, limitations may arise because of possible risks and restrictions on importing nonnative plants by the country in which experimentation is to be conducted (Vettraino et al. 2020). This challenge is likely to increase as the number of test tree species increases and phytosanitary measures for live plant trade become more stringent. Logistical requirements, such as planting, fencing, watering, and regular monitoring, pose an extremely important challenge. These may best be met by establishing reciprocal international agreements among trading partners (Kime et al. 2021).

Rather than relying on new plantings, botanic gardens and arboreta can provide information of possible new associations with adult trees. This was the case, for example, with London plane (*Platanus* x *acerifolia*) and polyphagous shot hole borer (*Euwallacea fornicatus*; Paap et al. 2018) and with pines (*Pinus* spp.) and pine aphid species (*Eulachnus brevipilosus* and *Essigella californica*; Redlich et al. 2019). Many botanic gardens are linked to the International Plant Sentinel Network (Barham et al. 2015), and their staffs can assist with surveys and access to data on historical occurrences of pests. Unfortunately, botanic gardens and arboreta typically contain only a few individuals per plant species, which limits the robustness of results, given the positive detected species–area planted relationship mentioned above (Branco et al. 2015). In addition, the most severe insect and pathogen impacts may no longer be present because dead or badly damaged plants are removed, so if not accurately registered, the information may be lost. Such damaged and stressed plants in nature sometimes provide the requisite susceptible food base or infection court for a new invasive species during its essential but highly tenuous establishment phase. The significance of this effect will likely vary with the specific biology and feeding guild of various insects, pathogens, and insect–pathogen complexes. Furthermore, botanic gardens are typically relatively manicured environments, so they may not provide the needed microsites, such as thatch for overwintering, for certain insects and pathogens, or they may not harbor the appropriate vectors of phytopathogens. Finally, some of the trees in arboreta are very large, which can make sampling difficult, expensive, and sometimes dangerous.

Large-scale plantations of nonnative tree species can also be used as sentinels. For example, *Eucalyptus* plantations in Brazil highlighted the risk of possible introduction of myrtle rust (*Austropuccinia psidii*) into other continents where members of the Myrtaceae are abundant, which, in fact, occurred (Roux et al. 2004, Carnegie and Pegg 2018). Large-scale plantations provide the advantages of many planted individuals, large areas encompassing different environmental conditions, and longer times since planting, all of which increase the likelihood of detecting problematic species (Wingfield et al. 2011, Burgess and Wingfield 2017). The longer time since planting allows more time for host shifts to occur and for irruptive insect and pathogen species to pass through extended periods of low abundance when detection is unlikely. Therefore, some of the challenges arising from manicured gardens are reduced in large-scale plantations. Conversely, plantation trees are commonly subjected to extensive genetic breeding programs, resulting in a relatively narrow genetic base that may not be representative of wild native plants. Where such genetic bottlenecks are severe, they can reduce the usefulness of plantations to assess susceptibility, resistance, and tolerance to various herbivores and pathogens. Also, only a small number of tree species are widely propagated as nonnatives in plantations, limiting potential hosts that can be tested.

Urban trees can be used effectively as sentinels, especially in coordination with other sentinel approaches (Wondafrash et al. 2021). Urban trees provide the advantages of including both native and nonnative species distributed over wide geographic and age ranges. They also include plants that are stressed by urban environments that may make them especially prone to attack by certain groups of insects and pathogens, adding to their value for early warning. For example, ornamental European *Betula* spp. planted in North America can serve as proxies for a potential invasion by *Agrilus anxius* in Europe (Petter et al. 2020). However, as with large-scale plantations, urban trees often have a relatively narrow genetic base that is not representative of their actual diversity. Also, despite the wide geographic range over which a popular urban tree species may be deployed, they are often planted in locally homogenous conditions, including manicured settings that may fail to satisfy a pest's life history requirements that would otherwise be met in forests.

Sentinel trees can be more useful for assessing risks that arise from some of the major causes of host mortality by invasive species than others. In particular, *ex patria* plantings are well suited for identifying threats that arise primarily from lack of coevolved host tree resistance (i.e., loss of bottom-up control). In contrast, *ex patria* plantings cannot predict effects of missing coadapted natural enemies in the imported region (i.e., loss of top-down control) because all the natural enemies are present in the source region where assessments are performed. The extent to which this matters depends on biological attributes of the insect or pathogen. For example, enemy release is rarely documented as the primary basis for pathogens that cause little or no impact in their native region but become damaging in an introduced region, as is evidenced by examples where reintroducing native host germplasm into resistance breeding substantially reduced losses (Showalter et al. 2018). With insects, enemy release appears generally more important with folivores and sap feeders than with woodborers, as is evidenced by the higher success rate of classical biological control with the

former two than latter feeding guilds (Showalter et al. 2018). In addition, *ex patria* plantings cannot predict pest problems that arise from novel microbial associations, such as when an introduced pathogen acquires a new vector or *vice versa*, an introduced insect creates new infection courts for a native pathogen, or an introduced pathogen exploits infection courts created by native insects (Showalter et al. 2018, Santini and Battisti 2019). Likewise, *ex patria* plantings cannot predict indirect effects such as increased susceptibility to or other facilitation of native pests.

Laboratory assays using plant parts or seedlings

A potentially powerful and logistically amenable approach to forecasting the impacts of specific insects or pathogens lies in artificially infesting or infecting potential hosts to determine degrees of susceptibility. Such screening involves testing tree species native to the importing region to putatively damaging biotic agents present in exporting regions. This is conceptually similar and complementary to using sentinel plantings, but instead challenges seedlings, plant parts (e.g., leaves, branches logs), or other forms of germplasm to species from targeted taxonomic or functional groups under controlled conditions. Assays may be performed either in the region of origin or in approved biosafety laboratories in the importing region. Assays with detached plant parts or seedlings avoid many of the logistical constraints of sentinel plantings in that they are relatively amenable to experimental control, standardized challenge, and replication. They are also amenable to rapid throughput of test combinations. In this regard, controlled screening may provide the most expeditious approach to assessing potential direct impacts (figure 3b).

The key assumption underlying the use of plant parts or seedlings is that the results can be extrapolated to predict injury to intact live trees, and of the age class used in nature. The extent to which that assumption is met may vary between pathogens and herbivores, among types and taxonomic groups of pathogens, and among herbivore feeding guilds. Also, the extent to which results represent relationships under natural conditions is modified by the degree to which exogenous biotic and abiotic stressors affect outcomes in open environments in each study system. As an example, environmental stressors tend to more strongly dictate the outcomes of tree interactions with wood-boring insects than folivores (Koricheva et al. 1998).

There are cases where the assumption that assays represent natural conditions can be met. These include certain pathogens that infect shoots or young tissues, such as some rust fungi. For example, the myrtle rust pathogen *A. psidii*, which is native to South America but has been introduced into many countries, has a wide host range and threatens both native forests and the global *Eucalyptus* industry (Glen et al. 2007). Numerous greenhouse studies using small plants have helped characterize the relative susceptibility of *Eucalyptus* spp. or important genotypes in advance of the pathogen's arrival (Roux et al. 2015). An example where such assays can be misleading involves the pine wood nematode *B. xylophilus*. Following extensive death of mature *Pinus* spp. in Japan (Mamiya 1983), experiments with seedlings indicated high susceptibility of many North American tree species, causing significant alarm (Dropkin et al. 1981). However, these results did not facilitate recognition that this pest is actually native to North America, where trees are highly tolerant under natural conditions (Wingfield et al. 1984). When the same *Pinus* spp. were assayed by inoculating larger trees, there was no evidence of disease (Wingfield et al. 1984). The key point is that *B. xylophilus* does not cause wilt disease in seedlings so using them as a proxy yields misleading results. A similar situation likely holds for vascular wilt diseases in which natural conditions require the pathogen to colonize tissues that are not yet developed in seedlings, as, for example, with various susceptibility studies of forest trees to *Ceratocystis* spp. (Roux et al. 2004). Such vascular wilt pathogens, including those associated with insect vectors, are some of the most damaging invasive species in the world (Ploetz et al. 2013).

Examples and considerations of in vitro and seedling assays. For pathogens, assays can be conducted by inoculating a variety of host tissues ranging from plant parts in Petri dishes to seedlings in greenhouses. For example, two studies (Lobo et al. 2015, Gross and Sieber 2016), using stem and leaf inoculations of young trees (60–170 centimeters and 8 years, respectively) across *Fraxinus* revealed genetic variation in susceptibility to the ash dieback pathogen *Hymenoscyphus fraxineus*. Similarly, extensive screening indicated that many common North American tree and understory species are susceptible to *P. ramorum* (Tooley et al. 2004, Tooley and Browning 2009, Jinek et al. 2011). The most appropriate method depends on the type of host–pathogen interaction and the lifestyle and biology of the pathogen.

Pathogen lifestyles can affect the optimal method of *in vitro* assays or even our ability to conduct them. Inoculation is relatively simple for some pathogens that can be propagated in culture (typically, necrotrophs and hemibiotrophs) or on host tissues (e.g., some obligate biotrophs such as rust fungi). Inoculation of some rust fungi such as *Austropuccinia psidii* on Myrtaceae (Roux et al. 2016) and *Melampsora medusae* on *Populus* (Hamelin et al. 1994) can be performed on seedlings or detached leaves. Because the economic host of these rusts are also the telial hosts, urediniospores can be produced in large numbers on susceptible plants and stored for assays. Some other examples include the pine pitch canker pathogen *Fusarium circinatum* or oomycetes such as *P. ramorum*, that can be easily grown and maintained to produce spores (Hodge and Dvorak 2000, Tooley et al. 2004, Tooley and Browning 2009, Jinek et al. 2011, Mitchell et al. 2013, Preuett et al. 2013). For other fungi however, such as obligate biotrophs that require alternate hosts, or pathogens that require an insect vector, *in vitro* inoculations can be much more challenging.

A variety of methods have been used to evaluate the host range of and relative susceptibilities to insects. These include

excised twigs with foliage for defoliators and sap suckers, and bark disks, logs, or branches for bark beetles, ambrosia beetles, and wood borers. Bark sections have been used to access the host ranges of several bark beetle species that attack mature trees on the basis of behaviors such as boring into the bark and establishing a gallery (Elkinton and Wood 1980, Raffa 1988, Walter et al. 2010, Hefty et al. 2018). Using this method, it was established that bark of *Pinus resinosa* elicits higher entry rates and longer gallery formation by *Orthotomicus erosus* than bark of other conifers (Walter et al. 2010). Assays using logs also allow assessment of reproductive success on different tree species. For example, *O. erosus* produced more offspring in logs of various North American pine and spruce species than fir, larch, and redwood species (Lee et al. 2008). Similar experiments using log sections were conducted to determine host preferences of *Anaplophora glabripennis* (Faccoli and Favaro 2016).

Seedlings can be used for several insect guilds. For example, twigs or branch tips were used to examine and rank the host range of the folivorous Eurasian nun moth (*Lymantria monacha*) on North American tree species and European species planted in North America (Keena 2003). A similar approach was used to determine if *L. monacha* and *L. dispar* pose threats to *Pinus radiata* (Withers and Keena 2001), which is widely planted worldwide. Caged, potted European conifer seedlings were exposed under quarantine conditions to Siberian moth (*Dendrolimus sibiricus*) larvae, which developed successfully on most of these species (Kirichenko et al. 2011), suggesting that host–plant availability would not limit its establishment and spread if introduced into Europe. Among insects that feed on stems of young trees, a field bioassay was conducted to determine the extent of maturation feeding on *P. radiata* by the invasive bark beetle *Hylastes ater* (Sopow et al. 2015). Likewise artificially infesting *C. fagisuga* eggs on potted seedlings and grafts, and trees in the field, has been used to identify scale-resistant lines for beech bark disease management and tree improvement programs (Koch et al. 2010, Koch et al. 2012). Challenges described by the authors include phenological variation among test insects and the need to ultimately relate scale densities to disease severity.

Advantages and limitations of in vitro and seedling assays. The major advantages of screening potential pests using *in vitro* or seedling assays are that they are performed under controlled conditions, can readily incorporate both positive (known hosts) and negative (known nonhosts) controls, can provide a range of environmental conditions, can be performed relatively rapidly, and are statistically replicable at relatively low costs (tables 4a and 4b). These assays can also be performed under quarantine conditions that confine nonnative species.

An additional advantage is that multiple host species and genotypes can be simultaneously tested with multiple pathogen isolates or insect races in randomly designed, replicated experiments. This can address species having genetic lineages and variants with different characteristics, and the diverse genotypes in natural pathogen and insect populations. For example, *Meterosideros* spp., native to New Zealand, are potentially threatened by the myrtle rust pathogen *A. psidii*, which has several races (Toome-Heller et al. 2020, Soewarto et al. 2021). Screening a diversity of *Meterosideros* and other Myrtaceae provenances to specific pathogen genotypes outside New Zealand can provide a robust estimate of the potential impact. Such extensive testing of host–pathogen genotype permutations is often not practical for sentinel plantings where smaller numbers of trees are typically used because of space and cost considerations, and even less so in botanic gardens where such screening was not their primary intent at planting. Furthermore, exposing sentinel and botanic garden trees to a fully representative range of pest genotypes may not be feasible because of biosafety considerations. The ability to statistically replicate a multiplicity of environmental combinations and species is a particularly valuable attribute of seedling and in vitro assays for evaluating relationships under future anticipated climatic conditions.

Despite their utility and speed, there are several important limitations to *in vitro* and seedling assays (tables 4a and 4b). In the case of pathogens, the environmental conditions required for infection are often unknown. Unfortunately, the most damaging invasive pathogens are often those about which we understand little basic biology because of their relatively low or unnoticed impacts in their native region. Conducting inoculations under the wrong or even suboptimal temperature or humidity conditions can generate false negatives. For example, inoculating *P. ramorum* spores onto hosts under conducive conditions often fails if the tissues are not first wounded, an extra step that may not represent natural conditions (Tooley et al. 2004, Tooley and Browning 2009, Jinek et al. 2011). Conversely, conditions that are overly conducive and do not reflect actual environments can yield exaggerated risk estimates. In addition, phenological factors that often play important roles in the timing of infection in nature are not easily emulated in growth chambers or greenhouses. With insects, results may vary with whether or not assays allow behavioral choice among test plants. In nature, mobile insects often have an opportunity to choose among several available tree species and individuals, but assays conducted as no-choice experiments elicit greater host acceptance (Raffa et al. 2002).

Pathogens and insects often do not act alone. Many rust fungi and sap-feeding insects require an alternate host to complete their life cycle. This can greatly complicate both the assays and the resulting risk assessment. The discovery of novel, unrelated, alternate hosts for pine rusts in Europe and North America illustrates this challenge to experimental design (McDonald et al. 2006, Zambino et al. 2007, Kaitera and Nuorteva 2008, Kaitera et al. 2012). Other pathogens require insect vectors or wounding agents to access their host, further complicating bioassays by requiring that both species be present

Table 4a. Relative advantages of typical in vitro and laboratory assays for susceptibility to insects and pathogens.

Advantages	Plant tissue assays (leaf and bark disks, cuttings, etc.)	Log sections	Seedlings
Can be done in laboratory under standardized conditions across a range of environmental settings	√	√	√
Do not rely on existing populations in nature being adequate for testing at time of interest	√	√	√
High replication easily attained	√		√
Many different plant species, provenances and candidate pests can be tested, even simultaneously	√	√	√
Young trees (seedlings, plantlets, saplings)	√		√
Mature trees	√	√	
Can be performed in facilities outside the area in which an organism of concern occurs. Allows for proactive approach.	√	√	√
Can yield very rapid results	√		

Note: Some rankings are in parentheses because the condition can be fulfilled in theory but is often not fulfilled in practice. For details, see the text.

Table 4b. Relative limitations of typical in vitro and laboratory assays for susceptibility to insects and pathogens.

Limitations	Plant tissue assays (leaf and bark disks, cuttings, etc.)	Log sections	Seedlings
May require an approved containment facility when testing outside the area in which candidate pests occur	√	√	√
Laboratory conditions may not be representative of environmental conditions in the field and therefore bias results	√	√	√
Defense responses may not occur as in intact live trees	√	√	
Results with seedlings may not reflect susceptibility of older trees and ontogenetic patterns of defense allocation.			√
Difficulties in administering and emulating proper levels and rates of infection/infestation because of species- and system-specific properties.	√	√	√
Interactions of pathogens with vectors or wounding agents in nature may be difficult to replicate	√	√	(√)
Deals solely with bottom-up trophic interactions: Cannot predict impacts that would arise from reduced top-down forces. Cannot forecast new insect–microbe associations that might occur in invaded region.	√	√	(√)
Requires some a priori knowledge of both which insects and pathogens are of most concern and fundamental attributes of their biologies, which is often lacking.	√	√	√

Note: Some rankings are in parentheses because the condition can be fulfilled in theory but is often not fulfilled in practice. For details, see the text.

and in appropriate stages. Some examples include Dutch elm disease, laurel wilt, and *Xylella fastidiosa*. Replicating vectored host–pathogen interactions in controlled environments adds complexity to risk assessment by introducing the dimensions of insect behavior, symbiotic relationships, and coinciding life stages. Another important consideration is that the rate of successful attack may depend on the number of attacking insects in gregarious species. Trees are often able to defend themselves against attack by low numbers of *Dendroctonus ponderosae* and *I. typographus*, but during outbreaks mass attacks by these beetles can exhaust and overcome tree defenses (Raffa 1988). Therefore, in systems where attack density plays an important role, *in vitro* assays with only a few individuals can underestimate host suitability.

Another important shortcoming of some seedling assays is that the assumption that seedlings are good surrogates for mature trees is not always met. This is particularly true for pathogens that colonize roots and spread via root-to-root contact or those that grow inside the woody tissues. This assumption is likewise often not met with bark, wood-boring and root collar insects. Many of these species show strong age and size relationships with host trees in nature. The underlying bases for such associations with mature trees involve both the physical dimensions needed to harbor brood and complex ontogenetic patterns of age-related defense (Boege and Marquis 2005, Barton and Koricheva 2010, Quintero and Bowers 2011, Erbilgin and Colgan 2012, Karinho-Betancourt et al. 2015).

The extent to which *in vitro* assays reflect natural conditions can also vary with feeding guild. Host preference rankings by folivores feeding on detached leaves or leaf disks often emulate defoliation rankings observed on trees (Robison and Raffa 1994). However, results with wood-boring insects may fail to capture important differences between healthy and stressed or dead hosts and to capture intraspecific variability. Many members of this guild prefer trees in a weakened condition, so substantial selectivity can be lost in dead tissues. For example, *Tomicus piniperda* successfully reproduced in a wide range of *Pinus* species logs (Eager et al. 2004). But its realized host range is much lower, and in healthy trees, it is largely confined to European species (McCullough and Sadof 1998, Morgan et al. 2004). Likewise, *D. ponderosae* had an approximately three times greater entry rate in bark disks than when caged onto the same live trees, and the rate of attack abandonment attacks was 12 times higher in live trees than bark disks (Raffa 1988). This suggests that some host defense mechanisms—particularly, actively induced chemical or physical defenses—that operate in live trees do not perform as well in excised tissue. Therefore, assays with bark disks or logs may be more indicative of host suitability from the standpoints of behavioral recognition, nutritional quality, and some aspects of constitutive defense rather than host susceptibility from the standpoint of beetles being able to overcome the integrated constitutive and induced defenses of live healthy trees.

The costs can also be an important consideration. Screening requires maintaining a relatively large number of viable and virulent pathogen cultures, insects, and candidate trees in order to encompass the variability present in natural populations. Also, any screening of regulated organisms outside their native range must be conducted in dedicated secured facilities, which can pose a significant limitation.

Finally, although laboratory assays are well suited for identifying new host associations, the extent to which results can be scaled up to predict an insect or pathogen's population-level performance in a new ecosystem may be constrained. This can be particularly problematic for those insect species whose dynamics are strongly affected by top-down and lateral, as well as bottom-up trophic interactions (Raffa et al. 2020). The extent to which that is a serious limitation may vary between pathogens and herbivores and among herbivore guilds.

Conclusions

Explicitly characterizing the underlying assumptions behind various approaches to forecasting potential impacts of nonnative insects and pathogens can help identify the optimal conditions for employing each approach, improve the integration and complementarity of their attributes, and better identify future research needs. None of the approaches we examined can, by itself, provide a high level of combined precision and generality to predict which species will have relatively minor versus severe effects on forest ecosystems, but conversely, each approach offers some particularly unique strengths. Each approach has substantial value, but each likewise differs in its strengths, limitations, and the extents to which various underlying assumptions are met.

The utility of each approach can be enhanced by better targeting the circumstances under which it is most likely to have the highest applicability and efficiency. For example, prior pest history provides greater predictive power when using information from previous invasions than on population dynamics in native regions. Major challenges to the latter arise from the vast number of unknown species, the limited biological knowledge on most known species, and the incapacity to extrapolate from population drivers in coadapted native to naive nonnative ecosystems (Liebhold et al. 2012, Ayres et al. 2014, Eschen et al. 2015a, Hughes et al. 2017, Bonello et al. 2020). Likewise, models attempting cross-taxa comparisons of pest–host interactions appear more promising when they incorporate phylogenetic than trait-based patterns. Trait-based patterns may be better suited for predicting transport and establishment than for predicting impact (Brockerhoff and Liebhold 2017, Liebhold et al. 2021, Mally et al. 2022). Similarly, *ex patria* sentinel plantations appear more likely to detect species that would emerge as important pests in naive ecosystems because of a loss of bottom-up than to detect those emerging because of top-down controls. The former include most fungi and wood-boring insects, whereas the latter include most insect defoliators (Showalter et al. 2018). *Ex patria* plantings

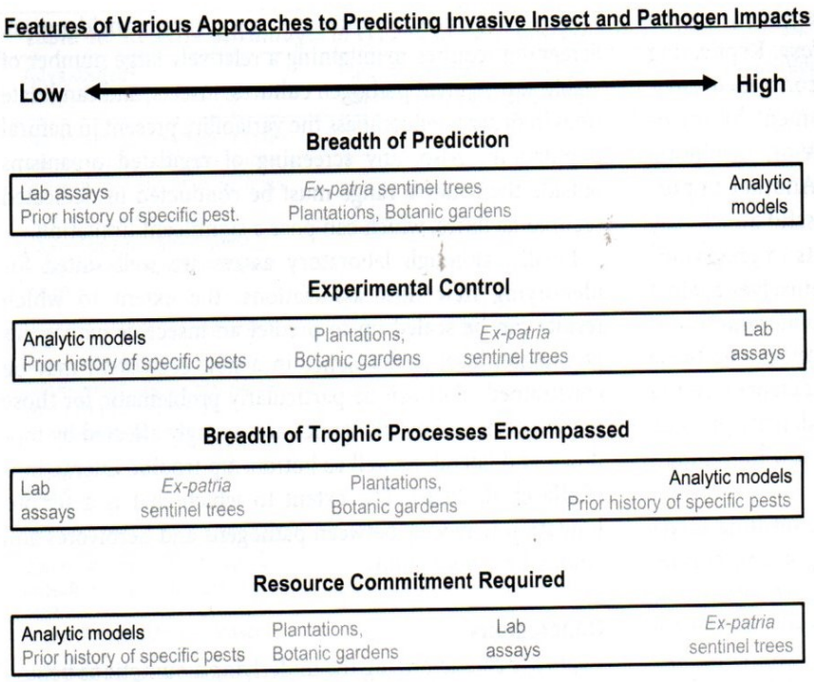

Figure 4. Different approaches to predicting impacts of invasive forest insects and pathogens vary in several key attributes such as the breadth of the predictions they generate, the extent to which they are amenable to experimental control, the components of trophic web interactions they incorporate, and the resources required to implement and maintain them. For example, several approaches involve case by case evaluation, whereas analytical models yield general predictions about host and pest traits, phylogenies, and genomes. Likewise, some approaches can provide high experimental control under defined conditions and can replicate defined genotypic variation across environmental gradients, whereas others are purely correlative or historical. The trophic relationships assayed or simulated likewise range from single, direct host–pest interactions in the native region to altered multitrophic relationships in the nonnative region. In general, there are trade-offs in the breadth of prediction, the degree of experimental control, and ecological complexity among the approaches. See the text for a full discussion and examples. For brevity, ex patria* sentinel trees *refers to plantings specifically designed for pest assessment;* plantations *and* botanic gardens *refers to botanic gardens, arboreta, commercial plantations, and urban trees that contain various mixtures and combinations of nonnative and native plants. All rankings are on a relative scale.

specifically aimed at detecting potential pests are also most applicable for insects and pathogens that are not primarily associated with relatively older trees. In a similar fashion, controlled assays are most promising for species whose performance on seedlings and detached parts more closely reflects their performance on live mature trees. This suggests they may be more reliable for insect folivores and sap feeders than wood-boring insects or vascular wilt pathogens (Wingfield et al. 1984, Robison and Raffa 1994). Beyond these general biological attributes, each approach has various logistical, operational, and statistical advantages and difficulties.

In addition to helping identify the conditions under which each approach is most likely to contribute, our analysis also provides a framework for identifying and enhancing complementarities and synergies among different approaches. Figure 4 illustrates the major approaches along four independent axes: the breadth of predictions they allow, the degree of experimental control and replication they provide over a range of genotypes and environments, the extent and variety of trophic processes incorporated, and the anticipated costs. As used in this figure, the *extent of trophic processes incorporated* refers to higher-scale factors such as natural enemies, other plant species that either serve as obligately alternate or facultatively additional hosts or mediate tritrophic interactions, symbiotic associations, environmental, spatial, and density-dependent mediators, and so on. This conceptual framework provides a basis on which complementarity can be overlaid, synergism can be fostered, and optimal sequences can be developed. For example, previous reports of pest activity and analytic models jointly differ from *ex patria* sentinel plantings and laboratory assays in that the former are historical and associational, whereas the latter are based on direct experimentation. Similarly previous reports of pest activity and laboratory assays differ from analytic models and sentinel plantings in that the former rely more heavily on prior knowledge of candidate species, whereas the latter require fewer assumptions about which insects or pathogens require emphasis. In a similar vein, analytic models and laboratory assays are more amenable to statistical analysis than previous reports of pest activity and observations in botanic gardens. In some cases, complementarity can best be achieved in a sequential fashion, such as prior reports of pest activity providing critical raw data for analytic models and, in others, more concurrently, such as the conceptual overlap between *in patria* plantings being aligned in a concentrated but geographically limited design (e.g., hubs) versus a more extensive but less targeted manner (e.g., regional surveys of prior pest activity).

In addition to the complementarity among approaches, there also can be improved complementarity within different subcategories of approaches. For example, it may be beneficial to incorporate several different types of models into single predictive systems, and refining current phylogenic approaches into more specific genomic models may provide avenues to reintroduce trait-based patterns into

predictions. Likewise, there are substantial opportunities to integrate the strengths of various types of sentinel trees, such as the extent to which each can incorporate bottom-up versus top-down constraints, their maintenance costs, and their extent amenability to statistical analysis (tables 3a and 3b, figure 4). Progress in linking information that arises from various forms of sentinel plantings is already underway (e.g., Barham et al. 2015, Morales-Rodriguez et al. 2019). Finally, some limitations to individual approaches are largely inherent to the method, but others, such as the difficulties in extrapolating from young to mature trees, can be at least partially alleviated as plantings age, providing there are long-standing commitments to their support.

It is also worth considering how and when the complementarity of approaches could have provided better information in case studies that resulted in either significant tree loss or overestimated risk. For example, the associations of both *Agrilus planipennis* and *A. glabripennis* with native hosts in their native Asian range is primarily limited to severely stressed or dead trees, and so would not be forecasted as potentially important pests on the basis of their dynamics there. However, in both cases, they kill or injure live trees of North American origin planted in Asia (*Fraxinus pennsylvanica* and *Acer saccharum*, respectively; Wei et al. 2004, Yang et al. 2015, Dang et al. 2022), which would have raised alerts and subsequent testing had the North American trees been fully used as *ex patria* sentinels. An example in the opposite direction involves the establishment of *S. noctilio* in the northeastern United States. It has not become problematic on native trees there, despite being a pest of commercial plantations of pine species from western and southern North America in the southern hemisphere (Ciesla 2003). Likewise, *T. piniperda* established in North America, but is largely limited to plantings of European species and only highly stressed individuals of native species. The latter two cases illustrate the limitations of extrapolating from the nutritional suitability of logs to the full defensive capacities of live trees. Given the high degree of stochasticity in how insects and pathogens interact with hosts and other ecological forces in new regions, we currently lack a sound basis for deciding on the best use of negative data. Does it truly mean no risk? Should some jurisdiction decide not to implement protective measures on the basis of negative test or model results, and if so, who should make such decisions? Also, might the full impact of an established, currently low-impact species such as *S. noctilio* be still pending if, for example, its initial establishment in North America eventually facilitates transport to other parts of the continent that contain highly susceptible hosts such as *P. radiata*, *Pinus contorta*, *Pinus ponderosa*, *Pinus taeda*, and *Pinus elliotti*?

The various forecasting approaches also vary in their sensitivity to the manner in which *impact* is defined. In agroecosystems management objectives are relatively straightforward despite different opinions in how to achieve them, so the impact can be calculated in terms of decreased quantity or quality of yield or increased costs of countermeasures, such as pesticide applications and quarantines. In contrast, quantifying the impacts on forest values must consider the many different ways that trees are valued. Forest ecosystems provide multiple and, at times, competing economic, ecological, recreational, and aesthetic services, and therefore different sectors of the public value management objectives and desired outcomes differently. Therefore, devising broadly accepted, objective, quantitative scales of an impact is highly challenging. This is less of an issue with sentinel plants and laboratory assays that primarily measure direct impacts on the host than with prior pest history and analytical models that deal with the full consequences of establishment. Even in the former two approaches, however, the choice of which tree species to plant or screen is highly value laden, with the current emphasis largely prioritizing commercially desired species.

Biological invasions are interacting with rapid climatic changes that alter the environmental template on which new species associations interact. Precipitation patterns are changing dramatically to include both increased flooding and drought, which can greatly affect tree susceptibility to pathogens and insect herbivores, as well as interactions with natural enemies such as entomopathogens (Kolb et al. 2016). Warming temperatures are also changing the projected geographic ranges of established and future nonnative insect and pathogen species, requiring that both additional host species and expanded environmental conditions be considered. Although biological invasions are most commonly associated with human transport, elevated temperatures add another dimension to the challenge by allowing native species to migrate into and establish at higher latitudes and elevations than historical norms (Parmesan 2006). Once established in newly colonized ecosystems, insects and pathogens encounter evolutionarily naive host species and populations, novel trophic webs, and new symbiotic associations, raising the same types of concerns and uncertainties as following direct human introduction (Raffa et al. 2015). Our framework can help address the interacting challenges posed by these separate components of global change. Taken together, ongoing climatic changes require that the integration of forecasting approaches we propose be viewed as requiring continual updating rather than being single-time assessments. For example, general predictive models can be applied rapidly to simulate new and projected climatic conditions, and the resulting outputs can be directly incorporated into controlled assays and specifically monitored in various types of sentinel plantings.

Future research is needed to address some critical gaps in our abilities to forecast the impacts of invasive pests in natural, commercial, and urban forest ecosystems. Some of the major challenges include refining the statistical tools and estimates of sample size needed for reliable forecasting by the various approaches we describe, improving the reliability, breadth, and efficiency of bioassays, gaining deeper insight into the genomics of pathogenicity and how some microorganisms transition from saprophytic to pathogenic

lifestyles, and improving our understanding of how results from bioassays and plantings can be scaled up to ecosystem- and landscape-level dynamics. Likewise, we need better targeting, alignment, and synergizing of predictive approaches and methods for more rapid and complete information transfer across jurisdictional boundaries. Because novel insect–symbiont–host associations have proven particularly damaging and difficult to forecast, new paradigms are needed to better incorporate multipartite interactions, cofactors, and other complex relationships than traditional approaches (Feau and Hamelin 2017, Koskella et al. 2017). Additional research especially needs to address components of species interactions that have particularly high elements of stochasticity. For example, our current understanding of coevolutionary processes can provide good *post hoc* explanations for why a nonnative insect or pathogen either does not possess the requisite preadaptations to effectively use a novel host (i.e., low impact) or why a naive host lacks the coadapted defenses needed to repel attack (i.e., high impact), but it cannot predict which of the many wide-ranging outcomes will occur. In this regard, we need better understanding of which findings to date are largely descriptive and system-specific versus which are more normative, a knowledge gap that our synthetic approach can hopefully help narrow. Therefore, we need realistic assessments as to how general our predictions can ever reliably become, versus to what extent biological diversity dictates that each system has its unique elements that cannot be broadly extrapolated without generating unacceptable risk.

Plant protection agencies largely rely on the information and predictions provided by the approaches outlined above to develop pest risk analyses, so further research could reduce some of the uncertainties in their assessments. Here we highlight the benefits of more substantial incorporation of multiple, complementary approaches into our routinely administered regulatory frameworks. As one example, installing *in patria* plantations guided by prior pest history and general predictive models at exporting commercial hubs may be a prudent a requirement, alongside existing requirements of pest-free areas or sites of production and preexport phytosanitary treatments. Similarly, it may be useful for plant protection specialists to have input into a broader set of governmental policies such as protection of genetic resources (Mallapaty 2022) that could inadvertently put severe constraints on sentinel plantings and multigenotype screening, and that alternate complementary approaches to be in place if needed and their limitations proactively identified (figure 4).

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