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Forest Insect Biosecurity: Processes, Patterns, Predictions, Pitfalls

Helen F. Nahrung,^{1,*} Andrew M. Liebhold,^{2,3}
Eckehard G. Brockerhoff,⁴ and Davide Rassati⁵

¹Forest Research Institute, University of the Sunshine Coast, Sippy Downs, Queensland, Australia; email: hnahrung@usc.edu.au

²US Forest Service Northern Research Station, Morgantown, West Virginia, USA; email: andrew.liebhold@usda.gov

³Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Czech Republic

⁴Forest Health and Biotic Interactions, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland; email: eckehard.brockerhoff@wsl.ch

⁵Department of Agronomy, Food, Natural Resources, Animals and the Environment, University of Padova, Italy; email: davide.rassati@unipd.it

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*Corresponding author



Keywords

biological invasions, eradication, non-native species, pathways, phytosanitary measures, surveillance

Abstract

The economic and environmental threats posed by non-native forest insects are ever increasing with the continuing globalization of trade and travel; thus, the need for mitigation through effective biosecurity is greater than ever. However, despite decades of research and implementation of preborder, border, and postborder preventative measures, insect invasions continue to occur, with no evidence of saturation, and are even predicted to accelerate. In this article, we review biosecurity measures used to mitigate the arrival, establishment, spread, and impacts of non-native forest insects and possible impediments to the successful implementation of these measures. Biosecurity successes are likely under-recognized because they are difficult to detect and quantify, whereas failures are more evident in the continued establishment of additional non-native species. There are limitations in existing biosecurity systems at global and country scales (for example, inspecting all imports is impossible, no phytosanitary measures are perfect, known

unknowns cannot be regulated against, and noncompliance is an ongoing problem). Biosecurity should be a shared responsibility across countries, governments, stakeholders, and individuals.

1. INTRODUCTION

Non-native forest insects cause significant economic, ecological, and social impacts through losses to production, trade, and asset values; costs of control measures; and reduced biodiversity (6, 19). Consequently, substantial investments globally focus on mitigating the arrival and establishment of additional non-native species through biosecurity measures designed to minimize the adverse impacts of forest pests while facilitating the global movement of commodities and people (70).

Insect invasions occur across four successive stages, arrival, establishment, spread, and impact (Figure 1), each with different mitigation measures, priorities, and economic benefits (41, 96, 151). The mitigation measures form the biosecurity continuum, with preborder (offshore), border, and postborder interventions (Figure 1) designed to reduce the movement, establishment, and spread of non-native insects. However, despite decades of research on and implementation of biosecurity measures, invasions continue (131) and may be accelerating (130).

Forestry is one of the few industries with specific international regulations intended to mitigate insect invasions (72). In addition, the non-native insects impacting production forestry, amenity trees, and natural forest systems are numerous and relatively well understood (e.g., 6, 24, 109, 126). In this article, we use non-native forest insects as a model to review strategies used to mitigate invasion processes across the biosecurity continuum and to identify possible gaps that weaken the successful implementation of these strategies.

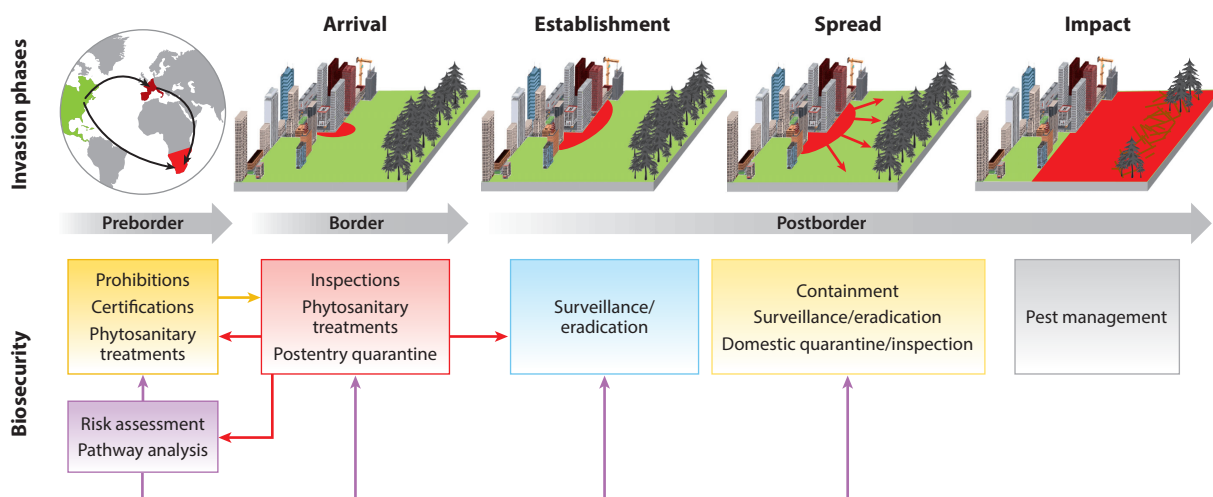


Figure 1

Phases of the biosecurity continuum (*gray arrows*) and biosecurity measures (*colored boxes*) corresponding to the different phases of the invasion process for non-native species introduced from their native range (*green area* on the map) to a new country (*red area* on the map) directly or via a bridgehead country (*dark red area* on the map). Arrows linking colored boxes represent the benefits that a given measure or set of measures can have for other biosecurity measures.

1.1. Origin

Insect invasions can originate from within a species' native range or from a previously invaded range (i.e., bridgehead introductions; 12) (**Figure 1**). For example, the wood wasp *Sirex noctilio* has a complex invasion history comprising separate introductions from its native range and bridgehead introductions among almost all invaded ranges (17). In contrast, global spread of the gall wasp *Leptocybe invasa* proceeded via bridgehead introductions (37), while invasions of the cerambycid beetle *Anoplophora glabripennis* mainly proceeded via repeated introductions from its native range (77).

1.2. Arrival

As is the case for all non-native species (131), international trade is the primary driver of accidental introduction of forest insects (106). Arrivals are rarely wind assisted (154); imports of live plants, wood, and wood packaging material (WPM) are the most important forest insect invasion pathways, followed by hitchhiking on nonhost cargo or conveyances and movement of passengers and mail (24, 106). Increased imports are thus associated with greater likelihood of non-native species introduction (98, 121, 150).

1.3. Establishment

The role of propagule pressure (number of individuals and frequency of arrivals) in invasion success is well-recognized (23, 134). The number of individuals required to establish a new population is influenced by Allee effects and reproductive strategies: Species that reproduce parthenogenetically (e.g., *L. invasa*) or via sib-mating (e.g., the ambrosia beetle *Eurwallacea fornicatus*) may require lower propagule pressure to establish (2). Establishment is also contingent on suitable climatic conditions, a lack of competitors and natural enemies, and suitable host plants in the area of introduction, all of which may be influenced by temporal and stochastic factors (87, 112). Urban areas may facilitate forest insect establishment (20, 111) because of high arrival rates via ports and airports and the presence of a wide variety of possible host tree species grown as ornamental trees.

1.4. Spread

Once established, non-native species expand their geographic ranges via natural and anthropogenic dispersal; in particular, long-distance spread largely arises from accidental movement by humans (e.g., 55). For example, movement of infested firewood likely facilitated the rapid spread of several forest pests (135), including *E. fornicatus* in South Africa (148) and the buprestid beetle *Agrilus planipennis* in North America (108). Population expansion into uninvaded areas requires similar conditions as for establishment, including suitable hosts and climatic conditions.

1.5. Impact

The final—and most subjective and context-dependent—invasion stage is impact. This can be described in economic (yield, trade, asset values), ecological (ecosystem services, biodiversity, biomass, carbon), social (health, well-being, amenity values), and cultural (iconic, traditional use species) losses and in costs of management. Most established non-native forest insects cause no measurable impact (24, 109); non-native wood- and phloem-boring insects tend to have the highest economic and social costs in forest systems (6, 35). Two such forest borer pests, *Ag. planipennis* and *An. glabripennis*, are listed among the top 10 of all invasive species (including weeds and vertebrates) for postinvasion management costs (34). These, along with the spongy moth, *Lymantria dispar*, and the balsam woolly adelgid, *Adelges piceae*, are among the purportedly most costly non-native insects worldwide (34, 19).

Sirex noctilio:

sirex woodwasp
(Hymenoptera:
Siricidae); the most
important invasive pest
of pines in the
southern hemisphere

Leptocybe invasa:

eucalypt gall wasp
(Hymenoptera:
Eulophidae);
presumed native to
Australia and invasive
on eucalypts in >40
countries

Anoplophora

glabripennis: Asian
longhorned beetle
(Coleoptera:
Cerambycidae); a
wood-borer invasive
on hardwoods in
North America,
Europe, and Japan

Wood packaging material (WPM):

pallets, crates,
dunnage, boxes, etc.
used for transport of
numerous
commodities and
products in
international trade

Eurwallacea fornicatus:

polyphagous shot hole
borer (Coleoptera:
Curculionidae);
ambrosia beetle
invasive in South
Africa, the United
States, and Israel

Agrilus planipennis:

emerald ash borer
(Coleoptera:
Buprestidae); invasive
in North America and
Europe, highly
destructive to *Fraxinus*
spp.

Lymantria dispar:
spongy moth
(Lepidoptera:
Erebidae); two of three
subspecies are invasive,
and polyphagous
larvae feed on
angiosperms and
conifers

Adelges piceae:
balsam woody adelgid
(Hemiptera:
Adelgidae); sap-feeder
invasive from Europe
on fir in North
America

Pest risk assessment:
evaluation of the
probability of
introduction, spread,
and economic impact
of a pest

Pest risk analysis:
evidence-based
determination of
whether an organism
is a pest that should be
regulated and that
requires phytosanitary
measures

2. PREORDER BIOSECURITY

Biosecurity measures aimed at preventing arrival are considered more cost effective than measures implemented during later invasion phases (34, 122), although identifying the optimal invasion stage for intervention is complex and dependent upon several biological factors (e.g., reproduction and dispersal rates) and economic factors (e.g., projected impacts, control costs) (44, 151). Preventative measures focused on populations before they reach the border include prohibitions on importation of certain plants or commodities, certifications that imported materials are free of prohibited organisms, and phytosanitary treatments, all of which are underpinned by pest risk assessment and pathway analysis (Figure 1).

2.1. Risk Assessment and Pathway Analysis

Predicting which forest insect species, groups of species, and pathways pose a biosecurity risk and warrant intervention is of considerable benefit (70, 86, 88). Pest risk analysis aims to identify biosecurity risks, justify preborder regulatory measures, and prioritize border and postborder biosecurity activities (99) but can be confounded by new source pools (132), taxa that are undescribed or of no impact in their native range (37, 126), and unregulated pathways such as smuggling (91).

To evaluate biosecurity risks associated with importing particular goods, countries conduct risk analyses, which are also required to ensure that phytosanitary measures (see below) comply with the Agreement on the Application of Sanitary and Phytosanitary Measures (SPS Agreement) of the World Trade Organization (110). Risk assessments focusing on pathways instead of individual species can address a range of taxa that are moved with the same imported goods or transport-related objects and assist with prioritizing border and postborder activities. For example, generically assessing risks associated with WPM addresses the many species that are moved via this pathway (73, 88), including those not yet recognized as damaging invaders.

Risk assessments typically focus on a limited number of individual unwanted species assessed to have a high likelihood of invasion and impact (91). Prediction can be aided through sentinel plantings in potential source countries (46) to determine which endemic insects in source countries attack sentinel species from the destination country. Evaluating biosecurity risk is difficult, requiring knowledge of habitat and climatic suitability and the likelihood of pest arrival, establishment, spread, and impacts (76, 149). Predicting any one of these elements is challenging because of methodological difficulties and because most potential invaders are not well-studied or may be previously unknown to science (e.g., 37). Furthermore, such risk assessments overlook species with no prior record of invasion or damage. For example, *Ag. planipennis* and *An. glabripennis* were not considered high risk at the time of their first invasions (48).

Fewer than 20 years ago, the scientific discipline of invasive species risk assessment was in its infancy (4). Now, risk models can incorporate host availability, climatic suitability (82, 149), estimates of arrival risk from border interception records (144), and potential impact, combining multiple risk predictors within an integrated suite of models (e.g., 76). Where information on particular risk predictors is lacking, aggregated assessments made by specialists (structured expert elicitation) can provide improved estimates (63)—or not (33).

2.2. Regulatory Frameworks

Prohibitions are a simple and effective approach for preventing non-native species arrival. Because trade in live plants is a common pathway for forest pest invasions, many countries ban importation of plant genera that are hosts of high-risk pests (45). Some countries implement blacklists of prohibited plant genera, while others implement more restrictive whitelists allowing only importation of genera that are considered low risk. In many cases, countries ban imports of live plants

but allow imports of seeds or cultured plant tissue; many countries ban importation of any plant with soil (45). However, import prohibitions interfere with free trade, are often opposed by commercial interests, and may be challenged by exporting countries (93). The SPS Agreement was, in part, implemented to circumvent countries using prohibitions as false justification for protectionist barriers to trade, requiring risk to be scientifically documented (110).

Certification is a preborder approach to prevention that is intended to mitigate barriers to trade between exporting and importing countries. In 1952, the International Plant Protection Convention (IPPC) implemented a system of phytosanitary certification (28) under which all shipments of plants or plant products must be accompanied by a phytosanitary certificate issued by the exporting country. This certificate verifies that the shipment meets phytosanitary requirements set by the importing country (3, 113). While this system places responsibility on the exporting country and creates incentives for reducing pest loads, it has practical limitations related to the detection of pests, particularly in large shipments. The IPPC also recognizes a process by which exporting countries can certify the pest-free status of parts of their country to facilitate exports (113, 124).

Phytosanitary treatment of imports plays a key role in preborder biosecurity, often allowing high-risk commodities to be safely imported (1, 64). These treatments are typically specified by the importing country and may comprise physical or chemical treatments that kill unwanted organisms. For example, many countries require chemical treatment (typically fumigation with methyl bromide or phosphine) of imported roundwood to prevent introduction of bark- and wood-boring insects (107, 113). Similarly, heat treatment, kiln drying, and bark removal can mitigate risk associated with the importation of wood products (1).

WPM accompanies a variety of cargo and poses considerable risk as a pathway for introductions of forest insects (106). Although some countries had already mandated phytosanitary treatments for wood packaging, the IPPC recognized the universal nature of this risk and implemented a harmonized standard, International Standards for Phytosanitary Measures (ISPM) 15 (54, 60), requiring either heat treatment or fumigation of all WPM moved in international trade. The standard includes a system for certifying treatments with a stamp imprinted on wood packaging. Inspection of ISPM 15–stamped WPM indicates that the standard, when correctly applied, eliminates most quarantine risks (60, 157), although failures occur when treatment is not conducted appropriately, or when certification is fraudulent, and treatment is not conducted at all (60, 61). However, the economic benefits of reduced pest damage outweigh the costs of ISPM 15 implementation (88). Measures under ISPM 36 (52), governing plants for planting, and ISPM 39 (53), governing movement of wood, also reduce risks of forest insect invasions.

3. BIOSECURITY AT THE BORDER

3.1. Inspection

Visual inspection of imports is widely used by national plant protection authorities to detect unwanted organisms and to verify compliance with phytosanitary measures (45, 152). In addition, records of species intercepted during inspections provide valuable information about pathway risks and species transported with imported goods (23, 80, 144). This information can inform risk assessments and ultimately justify establishment of new regulatory measures (**Figure 1**). However, inspection of imports is not a phytosanitary treatment as such because only a small proportion (typically 1–2%) of imports is inspected (23, 45). Furthermore, inspections cannot detect all infestations, and this slippage can be substantial (91). The effectiveness of visual inspection is constrained by limited detectability of some species and life stages, including those concealed inside plant tissues (e.g., bark beetles, wood borers), and by limited accessibility, such as in shipping containers (137). Targeting high-risk commodities, producers, or importers based on intelligence

from customs and phytosanitary agencies can increase the effectiveness of border biosecurity inspections. Inspections may also incentivize importers to reduce pest loads in shipments (136), particularly if infested shipments are refused entry.

3.2. Detection Tools

In theory, unwanted organisms might also be detected using methods such as X-ray imaging to see inside goods, detector dogs trained to detect odors associated with specific pests, or technologies that analyze acoustic signals or volatile organic chemicals that are characteristic of particular unwanted organisms (152). However, there are practical limitations to the availability and effectiveness of such methods. For example, compounds associated with living trees colonized by *Ag. planipennis* (153) might be difficult to detect during import inspections. Electronic noses have the potential to detect target species in border biosecurity but have technological and operational limitations, including sensor calibration and sensitivity constraints (117). Detector dogs are used successfully for detection of imports infested with *Anoplophora* species, and there is good potential for their use to detect *Ag. planipennis* (68, 69). Trained dogs can detect traces of juvenile and adult forms of the target species, showing high sensitivity (75–88% for *An. glabripennis* and 73.3–100% for *Ag. planipennis*) (68, 69). However, detector dogs need target-specific training and have a limited daily attention span, limiting the volume of imports that they can inspect, and their use is relatively costly. Acoustic detection of feeding, movement, or stridulation of organisms inside wood is possible (11, 32). For example, most bark beetles stridulate, producing species-specific sounds (10) that can be detected with microphones even when beetles are concealed in bark or wood—but only if the beetles are close (<20 cm) to the microphone, constraining the usefulness of acoustic detection of bark beetles in imported wood products (11). Similar limitations exist for the detection of other acoustic signals, and practical large-scale use of acoustic signals for inspection of imports is not yet possible. Sticky traps integrated with an attractant light source have been developed to detect insects within containers (103) but have been tested only under controlled conditions to date. Although such tools and techniques show promise, their operational use by port inspectors, phytosanitary personnel, and regulatory agencies is not widespread (117). Future technological advancements may help to overcome some of their limitations.

3.3. Phytosanitary Measures

Phytosanitary treatments (including fumigation, heat, cold, and radiation treatments) can be applied after arrival in the importing country when a regulated organism is detected (64); these treatments are governed by the regulatory framework mentioned above. For live plant imports, postentry quarantine in a dedicated quarantine facility for a period ranging from several weeks to years may be required by some countries and decreases the risk of importing unwanted organisms (45).

3.4. Diagnostics

Accurate and rapid diagnostic capacity to identify insects detected at the border—and in post-border surveillance (31)—underpins successful biosecurity. Identification of intercepted insects feeds into preborder risk assessments, postborder surveillance activities, and analysis of global patterns (144) and requires taxonomic expertise and access to reference collections and databases. Remote microscopy (online sharing of microscope imagery with remote taxonomic experts to assist with species identification) to rapidly access experts (141) and molecular approaches (125), including metabarcoding (101), are increasingly being used to support rapid diagnostics. In particular, molecular approaches are beneficial where insects are intercepted as immature stages that may foil traditional morphological identification methods.

4. POSTBORDER BIOSECURITY

4.1. Surveillance

If prevention of arrival fails, then the first opportunity to prevent permanent establishment of an invading species stems from effective surveillance (96). Because early detection is key to eradication success, surveillance for small, nascent populations is key to successful postborder biosecurity. As described above, risk assessment plays a key role in surveillance by identifying individual species, or groups of species, that have the greatest risk of establishment to enable targeted surveillance and mitigation (99) (**Figure 1**).

Detection surveys based on visual examination of trees in natural areas around high-risk sites (ports, airports, warehouses where containers are opened, nurseries, timber importers) have been a pillar of traditional postborder biosecurity (9). Increasing trade volumes, finite surveillance resources, and challenges related to tree inspections have highlighted the limitations of this approach, leading to the development of innovative methods to complement visual inspections (5, 84, 117). Traps baited with species-specific pheromones (e.g., 21) or pheromone blends and host volatiles to attract multiple species (e.g., 26, 50, 121), portable platforms for on-site molecular identification coupled with traditional genetic analysis (125), and citizen science campaigns (27) are already part of the biosecurity systems of several economically developed countries (e.g., 3, 30, 114) and will likely be adopted in developing economies (59). Stakeholder engagement increases surveillance capacity (31, 57), and surveillance of botanic gardens and sentinel trees in urban and high-risk areas enhances early detection (111).

The efficient allocation of resources for postborder biosecurity improves the success of detection (42, 43, 81). Strategies include tailoring trapping efforts according to identified high-risk pathways (e.g., 120, 121) and optimizing sampling efforts among surveillance locations (e.g., 14, 156). Balancing expenditure between surveillance and eradication is crucial for cost-efficient postborder biosecurity (16). If eradication is unfeasible due to logistics or cost, then surveillance will remain important to determine species' distributions, certify areas as free from particular pests, measure mitigation success, and aid in management decisions and reporting (78).

Surveillance is undergoing constant improvement due to technological advances and improved knowledge of attractants that can be exploited for pest detection. Increasingly rapid and user-friendly molecular methods will increase the speed and accuracy of identifications (116) and detect cryptic or undescribed species. Environmental DNA surveys and metabarcoding of trap contents can increase the chance of detecting non-native species, overcoming difficulties related to small species sizes, rapid life cycles, and cryptic behaviors (147). However, detection of non-native species via these methods has to be coupled with more traditional approaches (i.e., visual inspections) to understand the distributional range. Additionally, traps baited with a variety of attractants (e.g., pheromones, host plant compounds, light) can be integrated with cameras to improve surveillance efficiency (119), particularly if these cameras are self-reporting via connection to the internet.

4.2. Eradication

Eradication is the forced extinction of a population (97). There is a long history of successful (e.g., *L. dispar* in North America; 90) and unsuccessful (e.g., European house borer, *Hylotrupes bajulus*, in Australia; 30) eradications of invading forest insect populations, although rates of success have markedly increased over the past several decades (94, 139, 143). The size of the invaded area is a major determinant of the cost and probability of eradication success, as is the availability of sensitive detection tools (e.g., pheromone-baited traps) (143), although a few eradication programs have been successful even in their absence (94). Eradication is also more feasible for species that

Discount rate:

adjustment of cost estimates to align present, past, and future values

Anoplophora

chinensis: citrus longhorned beetle (Coleoptera: Cerambycidae); polyphagous on hardwood trees

do not disperse far from their natal host, such as *An. glabripennis*, which was successfully eradicated in parts of Europe and North America (21). These factors, along with the pest's potential impact, should be considered when deciding between eradication or containment (see below) (41).

The prospect of eliminating 100% of an invasive population may seem daunting. However, eradication is greatly assisted by strong Allee effects, whereby if populations are suppressed below a certain threshold, they will decline to extinction without further intervention (89, 90). Alternatively, it may be possible to facilitate eradication via pheromone-based mating disruption or by reducing dispersal by fragmenting the host matrix (8, 155) through selective tree removal. Many successful eradication programs have applied multiple types of treatments (e.g., host removal, microbial control, and sterile male releases, as used against the painted apple moth, *Teia anartoides*; 138) designed to interact to efficiently achieve eradication (15, 140).

In addition to being economically, logistically, and ecologically feasible (25), eradication programs need to be socially acceptable. Forest pests often initially establish in urban areas where residents may intensely scrutinize government-run surveillance or eradication campaigns. Eradication using chemicals, even those considered benign (e.g., species-specific pheromones) or with narrow toxicity (e.g., microbial pesticides), can result in public backlash, and tree removal can be particularly fraught (30, 90). Conversely, a do-nothing approach is also viewed as publicly unacceptable (104); public outreach and stakeholder engagement are increasingly recognized as key program components across the forest biosecurity continuum (3, 31), including garnering support for, or at least acceptance of, eradication measures.

4.3. Containment

As newly established populations spread into adjacent habitats, eradication becomes increasingly impractical and costly, but there may be substantial benefits from either stopping or slowing spread (containment) (133). In many cases, delaying (rather than stopping) spread produces economic benefit (e.g., *Ag. planipennis* in Canada; 67); a crucial aspect affecting the net benefit is the magnitude of the spread rate relative to the discount rate (44).

Containment comprises two general approaches: (a) directly or indirectly reducing movement of potentially infested materials from invaded to uninvaded regions and (b) surveillance for and eradication of nascent populations in uninvaded portions of the potential range (**Figure 1**). For forest insects, the most common approach to managing movement is through domestic quarantines. For example, the US Department of Agriculture prohibited the movement of firewood and nursery stock from the invaded range of *Ag. planipennis* until 2021, when the program was abandoned because its effectiveness (in slowing spread) was limited relative to its cost (145). In contrast, domestic quarantine to slow the spread of *Ag. planipennis* in Canada was deemed economically efficient (67). Domestic quarantines limited the spread of other forest insects; for example, in the United States, quarantine for *L. dispar* has been in place since 1912, requiring logs, firewood, nursery stock, Christmas trees, outdoor household articles, and vehicles (including recreational vehicles) to be inspected when moved outside of the previously invaded region (13). However, individuals moving such items may be unaware of these requirements, so efforts to educate the public could help to reduce risk.

Anoplophora chinensis has permanently established in Italy, but ongoing surveillance and eradication aim to contain its spread in Europe, primarily via visual detection of infested trees followed by destruction or systemic chemical treatment (21). This approach, much like the general surveillance and eradication described above, emphasizes detection of low-density populations and is more likely to be successful for species for which sensitive detection methods are available, such as Lepidoptera that can be detected at low densities using sex pheromone-baited traps. Perhaps the world's largest effort to contain the spread of a forest insect targets *L. dispar* in the United States

(95, 142). This species was accidentally introduced in 1869; a barrier zone, in place since 1999, has reduced spread by >50%. The program uses a grid of approximately 100,000 pheromone traps to locate isolated populations (formed via accidental transport of life stages by humans) just ahead of the expanding population front. Another 100,000 traps are placed in high-risk locations more distant from the invasion front. Eradication of isolated populations is usually triggered by positive trap captures in two successive years. The success of this program can be attributed in part to the species' limited natural dispersal (females are flightless) and the high sensitivity of pheromone traps.

4.4. Pest Management

Where prevention, surveillance, and eradication measures fail, and a pest establishes, management of the pest becomes the responsibility of government, industry, or private land holders (31). As the final stage in the biosecurity continuum to mitigate the impacts of insect invasions, management of established populations may provide the lowest economic return, estimated at 1:1–5 (122), although costs of damage caused by non-native species tend to outweigh expenditures on management (34, 36). Management options adopted for non-native forest insects include pesticides (including microbial insecticides), classical biological control (e.g., worldwide release of the egg parasitoid *Anapbes nitens* to control *Gonipterus* spp. eucalypt weevils; 129), inoculative biological control (e.g., use of pathogens against *L. dispar*; 62), breeding for resistance (e.g., deployment of eucalypt genotypes resistant to *Leptocybe invasa*; 128), and silvicultural manipulation (e.g., promoting tree health to reduce susceptibility to *Xylosandrus* spp.; 58). Development of more novel techniques, including kairomone-based push-pull strategies and RNA interference technologies such as gene silencing, also holds promise for management of invasive forest insects (58, 83).

5. COSTS AND BENEFITS OF FOREST BIOSECURITY

The direct costs of biosecurity implementation are borne across the mitigation activities described above. Preborder and border activities may simultaneously serve multiple industries and pests, while postborder activities become increasingly focused on particular tree species or ecosystems and particular pests within them. For example, Australia is implementing a postborder forest surveillance program aimed at preventing the establishment of multiple high-risk plantation, ornamental tree, and native forest pests (31), whereas eradication costs reflect the prevention of the establishment of a single species (e.g., US\$4.3M for giant pine scale in Australia; 30). Costs of biosecurity measures need to be weighed against the benefits of prevented impacts through economic cost–benefit analysis (151). The economic impacts of biological invasions (i.e., biosecurity failures) consist of ongoing pest management expenditures (e.g., suppression of *L. dispar* in the United States totaled over US\$12.3M in the five years to 2020; 146), as well as market and nonmarket losses. These losses include social costs (e.g., polyphagous shot hole borer is predicted to cause urban tree losses equivalent to 1% of South Africa's GDP; 35), yield loss (e.g., estimated losses from defoliation by *Gonipterus platensis* of 30% growth and 51% volume in Europe; 22), property value loss (e.g., sale prices decreased up to 1.6% due to *Adelges tsugae* in the United States; 66), and market access loss when importing countries refuse to trade certain goods (e.g., 118). Ecosystem service impacts are typically more difficult to quantify (18), and comparing impacts across different spatiotemporal, taxonomic, and socioeconomic scales is challenging.

Prioritization for allocation of limited resources for prevention, surveillance, and management activities is guided by the expected benefits of these activities, based on comparison of projected impact and biosecurity cost estimates. Conventional wisdom holds that prevention is the

Gonipterus spp:
eucalypt weevils
(Coleoptera:
Curculionidae)
belonging to a cryptic
complex of which
three species are
variously invasive
globally

Adelges tsugae:
hemlock woody
adelgid (Hemiptera:
Adelgidae); sap-feeder
invasive from East Asia
on hemlock and spruce
in North America

most cost-effective mitigation measure, with an estimated economic return of 100:1 (122); recent analyses revealed that costs of damage by invasive species outweigh investment in management (34, 36), and costs of management outweigh investment in prevention (34). However, long time lags between establishment and economic damage in some species result in impacts that may be diminished through discounting, and management during later invasion phases (e.g., eradication or containment) may sometimes be more cost efficient (42).

5.1. A Biosecurity Paradox?

Biosecurity suffers from its failures being evident but its successes being less visible or even invisible. Moreover, the more successful biosecurity is, the fewer new species establish or have an impact, and the less important it appears. While preborder, border, and postborder biosecurity efforts “undoubtedly reduce the entry of plant pests” (3, p. 6), it is difficult to measure their direct impact. For example, Australia has invested significantly in biosecurity measures targeting *L. dispar*, including strict preborder conditions, border inspections, and specific postborder surveillance. This species has never been detected postborder in Australia (39)—but whether this reflects biosecurity success, luck, or the failure of populations to establish is unknown. Similarly, where target populations are small, it may be difficult to attribute successful eradication to the efforts expended, rather than populations dying out regardless of intervention.

Biosecurity thus suffers from a lack of an alternative universe or counter-factual vision: The direct impact of biosecurity measures is difficult to observe or to test empirically because the risk posed by an experimental do-nothing control is deemed too great to include. Using data from countries that lack comprehensive biosecurity systems as an alternate universe is inherently flawed because comprehensive inventories of non-native insects are mostly lacking (127), and import volumes, commodities, and risk profiles vary. We term this the biosecurity paradox, i.e., the difficulty in attributing something that did not happen (e.g., a species that did not establish) directly to the measures employed to prevent it, or ruling out the probability that it would have happened in the absence of those measures. However, biosecurity risk is often characterized by low probabilities but large consequences of failure when a low-probability event does happen (76).

Uncertainty regarding the costs and benefits of national forest border biosecurity measures appears to have led, in general, to under-regulation, with wait-and-see approaches dominating phytosanitary policy decisions (65). Recent economic analyses have begun to incorporate a cost of inaction in response to invasions (e.g., 34), and such analyses often predict substantial additional costs incurred through delaying intervention.

5.2. But Does Biosecurity Work?

While we cannot directly quantify biosecurity success by knowing what it has prevented—particularly for arrival and establishment—its failures are evident. Despite biosecurity measures, new invasions frequently occur, and are even predicted to accelerate (130). While the increase in global eradication programs may indicate the inadequacy of upstream mitigation measures (139), it more likely reflects both improved eradication technologies and governments acting on positive cost-benefit analyses favoring eradication. Other evidence indicates successes in preventing establishments of certain insect groups. For example, regulation of plant imports has coincided with a decrease in marginal risk (per unit of imports) of non-native Hemiptera establishments and a decline in establishment of sap- and foliage-feeding insects in the United States over the past 150 (98) and 100 years (7), respectively. Similarly, worldwide implementation of ISPM 15 resulted in decreased arrivals of bark- and wood-boring insects, and decreased rates of establishment are expected (60, 88).

Australia's biosecurity system—among the strictest in the world (45, 122)—provides an estimated return on investment of 30:1 based on prevented losses over 50 years (38), and global estimates suggest that each dollar invested in invasive species management saves US\$53 in damage (34). Linear accumulation rates of non-native forest species establishing in Australia (109), New Zealand (24), and the United States (7), against a backdrop of virtually exponential increases in trade and travel (71) over the same timeframes, suggest that biosecurity is effective in these regions. However, the success of biosecurity may be counteracted by growing globalization opening new trade pathways and species source pools (132), the increasing movement of goods and people leading to ever-higher propagule pressure (23, 139), and differences in biosecurity stringency among countries (45).

The effectiveness of biosecurity mitigation measures at each step of the continuum is dependent on three factors: pest biology, effective tools or treatments (appropriate for pest biology), and compliance with implementation of these tools and treatments. For instance, to be effective, countries must comply with pest reporting and mitigation obligations in trade, importers must comply with required treatments, biosecurity agencies must use the best tools for detection, and individuals must comply with reporting and mitigation requirements.

6. A SHARED RESPONSIBILITY

Invasions by non-native organisms cause substantial impacts on forest resources in virtually every region of the world (18, 92). However, among world regions, there is considerable variation in the strength of biosecurity capacities (40, 45, 51). Given the ubiquity of bridgehead effects in the intercontinental spread of invading species, this global variation in biosecurity intensity represents a problem even to economically developed countries: Species may initially colonize countries with weak exclusion practices, but these regions can then act as sources of elevated propagule pressure and increase the probabilities of invasion elsewhere (123). Thus, although countries with more developed economies generally appear to be invaded more frequently than less-developed countries, world regions with limited capacities for biosecurity may represent a weak link in global efforts to control invasions (126).

This negative impact of limited biosecurity capacities in some countries suggests the potential global benefit from greater international cooperation; however, national and international politics can be an impediment. Historically, the primary role of national plant protection organizations has been to recognize risk and exclude pests from national borders (100). Simultaneously, national agro-economic interests seeking to expand agricultural exports may pressure national governments to facilitate these exports by arguing against the existence of risks to importing countries. Furthermore, there is a long history of nations using false claims of plant health risks to justify protectionist policies (i.e., prohibitions of imports) to protect domestic agro-economies from adverse impacts of competition with imported products (e.g., 29). The SPS Agreement is designed to promote free trade through eliminating protectionist policies by requiring importing countries to present scientific evidence of risk to justify prohibitions on imports (158). The IPPC also serves to promote cooperation on biosecurity by setting international biosecurity standards, requiring national governments to report on pest outbreaks and spread, and sponsoring biosecurity capacity building in countries with developing economies (74, 100).

Several authors have recognized the limitations posed by current biosecurity practices and proposed the development of a new international body or convention to better implement biosecurity at an international level, rather than a national level (72, 79, 115). These authors harnessed the analogy of the global spread of plant pests with the global spread of human pathogens to argue for a coordinated international body analogous to the World Health Organization to better coordinate national efforts at a global level.

The existence of sometimes lengthy lags between pest establishment and the onset of damage suggests a similarity between the prevention and management of non-native species and the global challenge and perfect moral storm posed by climate change, both of which require long-term proactive and collective cooperation (34). The inherent tensions between plant quarantine protocols and free trade and national agro-economic interests remain obstacles to implementation of a globally organized and optimized biosecurity program.

Despite these obstacles to truly cooperative biosecurity, small steps can provide incremental benefit. For example, there are opportunities for the development of more uniform invasion science research capacities among the world's major trading nations (105). Eyre et al. (49) highlighted the need to standardize methods and intensify inspections among different countries, even within the same continent, to enhance data comparability and reliability of interception records for use in risk analysis and phytosanitary decision-making. Greater opportunities clearly exist for data sharing among national plant protection agencies. Aichi Target 9 of the Convention on Biological Diversity required countries to report the occurrence of invasive species within their boundaries, but such reporting does not always occur (47). However, there are plans for a unified, globally comprehensive listing of all established non-native species (not limited to agricultural crop pests) (85, 102). Such comprehensive databases will allow biosecurity agencies to better identify risks, and invasion scientists to better understand drivers of new invasions (72). Similarly, Turner et al. (144) demonstrated how compilation of data on insects intercepted during port inspections from multiple world regions can be used to better understand invasion pathways worldwide. Sharing of data among nations, and among disciplines (75), perhaps offers the best immediate opportunities for more effective biosecurity via cooperation.

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LITERATURE CITED

1. Allen E, Noseworthy M, Ormsby M. 2017. Phytosanitary measures to reduce the movement of forest pests with the international trade of wood products. *Biol. Invasions* 19:3365–76
2. Allendorf FW, Lundquist LL. 2003. Introduction: population biology, evolution, and control of invasive species. *Conserv. Biol.* 17:24–30
3. Allison JD, Marcotte M, Noseworthy M, Ramsfield T. 2021. Forest biosecurity in Canada—an integrated multi-agency approach. *Front. For. Glob. Change* 4:700825
4. Andersen MC, Adams H, Hope B, Powell M. 2004. Risk assessment for invasive species. *Risk Anal.* 24:787–93
5. Augustin S, Boonham N, De Kogel WJ, Donner P, Faccoli M, et al. 2012. A review of pest surveillance techniques for detecting quarantine pests in Europe. *EPPO Bull.* 42:515–51
6. Aukema JE, Leung B, Kovacs K, Chivers C, Britton KO, et al. 2011. Economic impacts of non-native forest insects in the continental United States. *PLOS ONE* 6:e24587

7. Aukema JE, McCullough DG, Von Holle B, Liebhold AM, Britton K, Frankel SJ. 2010. Historical accumulation of nonindigenous forest pests in the continental US. *BioScience* 60:886–97
8. Barron MC, Liebhold AM, Kean JM, Richardson B, Brockerhoff EG. 2020. Habitat fragmentation and eradication of invading insect herbivores. *J. Appl. Ecol.* 57:590–98
9. Bashford R. 2008. The development of a port surrounds trapping system for the detection of exotic forest insect pests in Australia. In *New Advances and Contribution to Forestry Research*, ed. AA Oteng-Amoako, pp. 85–100. Rijeka, Croat.: InTech
10. Bedoya CL, Hofstetter RW, Nelson XJ, Hayes M, Miller DR, Brockerhoff EG. 2021. Sound production in bark and ambrosia beetles. *Bioacoustics* 30:58–73
11. Bedoya CL, Nelson XJ, Brockerhoff EG, Pawson S, Hayes M. 2022. Experimental characterization and automatic identification of stridulatory sounds inside wood. *R. Soc. Open Sci.* 9:220217
12. Bertelsmeier C, Keller L. 2018. Bridgehead effects and role of adaptive evolution in invasive populations. *Trends Ecol. Evol.* 33:527–34
13. Bigsby KM, Tobin PC, Sills EO. 2011. Anthropogenic drivers of gypsy moth spread. *Biol. Invasions* 13:2077–90
14. Blackburn L, Epanchin-Niell R, Thompson A, Liebhold A. 2017. Predicting costs of alien species surveillance across varying transportation networks. *J. Appl. Ecol.* 54:225–33
15. Blackwood JC, Berec L, Yamanaka T, Epanchin-Niell RS, Hastings A, Liebhold AM. 2012. Bioeconomic synergy between tactics for insect eradication in the presence of Allee effects. *Proc. R. Soc. B* 279:2807–15
16. Bogich TL, Liebhold AM, Shea K. 2008. To sample or eradicate? A cost minimization model for monitoring and managing an invasive species. *J. Appl. Ecol.* 45:1134–42
17. Boissin E, Hurley B, Wingfield MJ, Vasaitis R, Stenlid J, et al. 2012. Retracing the routes of introduction of invasive species: the case of the *Sirex noctilio* woodwasp. *Mol. Ecol.* 21:5728–44
18. Boyd IL, Freer-Smith PH, Gilligan CA, Godfray HCJ. 2013. The consequence of tree pests and diseases for ecosystem services. *Science* 342:1235773
19. Bradshaw CJ, Leroy B, Bellard C, Roiz D, Albert C, et al. 2016. Massive yet grossly underestimated global costs of invasive insects. *Nat. Commun.* 7:12986
20. Branco M, Nunes P, Roques A, Fernandes MR, Orazio C, Jactel H. 2019. Urban trees facilitate the establishment of non-native forest insects. *NeoBiota* 52:25–46
21. Branco S, Faccoli M, Brockerhoff EG, Roux G, Jactel H, et al. 2021. Preventing invasions of Asian longhorn beetle and citrus longhorn beetle: Are we on the right track? *J. Pest Sci.* 95:41–66
22. Branco S, Videira N, Branco M, Paiva MR. 2015. A review of invasive alien species impacts on eucalypt stands and citrus orchards ecosystem services: towards an integrated management approach. *J. Environ. Manag.* 149:17–26
23. Brockerhoff EG, Kimberley M, Liebhold AM, Haack RA, Cavey JF. 2014. Predicting how altering propagule pressure changes establishment rates of biological invaders across species pools. *Ecology* 95:594–601
24. Brockerhoff EG, Liebhold AM. 2017. Ecology of forest insect invasions. *Biol. Invasions* 19:3141–59
25. Brockerhoff EG, Liebhold AM, Richardson B, Suckling DM. 2010. Eradication of invasive forest insects: concepts, methods, costs and benefits. *N. Z. J. For. Sci.* 40:S117–35
26. Brockerhoff EG, Suckling DM, Roques A, Jactel H, Branco M, et al. 2013. Improving the efficiency of lepidopteran pest detection and surveillance: constraints and opportunities for multiple-species trapping. *J. Chem. Ecol.* 39:50–58
27. Brown N, Pérez-Sierra A, Crow P, Parnell S. 2020. The role of passive surveillance and citizen science in plant health. *CABI Agric. Biosci.* 1:17
28. Brunel S, Horn NM, Unger JG, Arntis R. 2013. Implementation of International Standards for Phytosanitary Measures no. 7 *Phytosanitary Certification System* and no. 12 *Phytosanitary Certificates*. *EPPO Bull.* 43:309–15
29. Cardwell R, Brewin DG. 2019. Blackleg or blackmail? Economics of the Canada-China canola trade dispute. *Can. J. Agric. Econ.* 67:251–60
30. Carnegie AJ, Nahrung HF. 2019. Post-border forest biosecurity in Australia: response to recent exotic detections, current surveillance and ongoing needs. *Forests* 10:336

31. Carnegie AJ, Tovar F, Collins S, Lawson SA, Nahrung HF. 2022. A coordinated, risk-based, national forest biosecurity surveillance program for Australia's forests. *Front. For. Glob. Change* 4:218
32. Chesmore D, Schofield J. 2010. Acoustic detection of regulated pests in hardwood material. *EPPO Bull.* 40:46–51
33. Clarke DA, Palmer DJ, McGrannachan C, Burgess TI, Chown SL, et al. 2021. Options for reducing uncertainty in impact classification for alien species. *Ecosphere* 12:e03461
34. Cuthbert R, Diagne C, Hudgins EJ, Turbelin A, Ahmed DA, et al. 2022. Biological invasion costs reveal insufficient proactive management worldwide. *Sci. Total Environ.* 819:153404
35. de Wit MP, Crookes DJ, Blignaut JN, de Beer ZW, Paap T, et al. 2022. An assessment of the potential economic impacts of the invasive polyphagous shot hole borer (Coleoptera: Curculionidae) in South Africa. *J. Econ. Entomol.* 115:1076–86
36. Diagne C, Leroy B, Vaissière AC, Gozlan RE, Roiz D, et al. 2021. High and rising economic costs of biological invasions worldwide. *Nature* 592:571–76
37. Dittrich-Schröder G, Hurley BP, Wingfield MJ, Nahrung HF, Slippers B. 2020. Invasive gall-forming wasps that threaten non-native plantation-grown *Eucalyptus*: diversity and invasion patterns. *Agric. For. Entomol.* 22:285–97
38. Dodd A, Stoeckl N, Baumgartner J, Kompas T. 2020. *Key Result Summary: Valuing Australia's Biosecurity System*. Melbourne, Aust.: Cent. Excel. Biosecurity Risk Anal.
39. Dominiak BC, Gillespie PS, Subasinghe R. 2013. Surveillance for Asian gypsy moth (*Lymantria dispar asiatica* L.) between 2005 and 2012 in New South Wales, Australia. *Plant Prot. Q.* 28:12–14
40. Early R, Bradley BA, Dukes JS, Lawler JJ, Olden JD, et al. 2016. Global threats from invasive alien species in the twenty-first century and national response capacities. *Nat. Commun.* 7:12485
41. Epanchin-Niell RS. 2017. Economics of invasive species policy and management. *Biol. Invasions* 19:3333–54
42. Epanchin-Niell RS, Bockerhoff EG, Kean JM, Turner J. 2014. Designing cost-efficient surveillance for early detection and control of multiple biological invaders. *Ecol. Appl.* 24:1258–74
43. Epanchin-Niell RS, Haight RG, Berc L, Kean JM, Liebhold AM. 2012. Optimal surveillance and eradication of invasive species in heterogeneous landscapes. *Ecol. Lett.* 15:803–12
44. Epanchin-Niell RS, Liebhold AM. 2015. Benefits of invasion prevention: effect of time lags, spread rates, and damage persistence. *Ecol. Econ.* 116:146–53
45. Eschen R, Britton K, Bockerhoff E, Burgess T, Dalley V, et al. 2015. International variation in phytosanitary legislation and regulations governing importation of plants for planting. *Environ. Sci. Policy* 51:228–37
46. Eschen R, O'Hanlon R, Santini A, Vannini A, Roques A, et al. 2019. Safeguarding global plant health: the rise of sentinels. *J. Pest Sci.* 92:29–36
47. Essl F, Latombe G, Lenzner B, Pagad S, Seebens H, et al. 2020. The Convention on Biological Diversity (CBD)'s post-2020 target on invasive alien species—what should it include and how should it be monitored? *NeoBiota* 62:99–121
48. Evans HF. 2010. Pest risk analysis—organisms or pathways. *N. Z. J. For. Sci.* 40:S35–44
49. Eyre D, Macarthur R, Haack RA, Lu Y, Krehan H. 2018. Variation in inspection efficacy by member states of wood packaging material entering the European Union. *J. Econ. Entomol.* 111:707–15
50. Fan JT, Denux O, Courtin C, Bernard A, Javal M, et al. 2019. Multi-component blends for trapping native and exotic longhorn beetles at potential points-of-entry and in forests. *J. Pest Sci.* 92:281–97
51. Faulkner KT, Robertson MP, Wilson JR. 2020. Stronger regional biosecurity is essential to prevent hundreds of harmful biological invasions. *Glob. Change Biol.* 26:2449–62
52. Food Agric. Organ. U. N. 2016. *International measures for plants for planting: International Phytosanitary Standard for Measures* 36. Rep., Int. Plant Prot. Conv., Rome
53. Food Agric. Organ. U. N. 2017. *International movement of wood: International Phytosanitary Standard for Measures* 39. Rep., Int. Plant Prot. Conv., Rome
54. Food Agric. Organ. U. N. 2021. *Regulation of wood packaging material in international trade: International Phytosanitary Standard for Measures* 15. Rep., Int. Plant Prot. Conv., Rome

55. Gilbert M, Grégoire JC, Freise JF, Heitland W. 2004. Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria obridella*. *J. Anim. Ecol.* 73:459–68
56. Gordh G, McKirdy S, eds. 2014. *The Handbook of Plant Biosecurity*. Berlin: Springer
57. Grant A, Pawson SM, Marzano M. 2019. Emerging stakeholder relations in participatory ICT design: renegotiating the boundaries of sociotechnical innovation in forest biosecurity surveillance. *Forests* 10:836
58. Gugliuzzo A, Biedermann PH, Carrillo D, Castrillo LA, Egonyu JP, et al. 2021. Recent advances toward the sustainable management of invasive *Xylosandrus* ambrosia beetles. *J. Pest Sci.* 94:615–37
59. Gupta K, Sankaran KV. 2021. Forest biosecurity systems and processes: an Indian perspective. *Front. For. Glob. Change* 4:699950
60. Haack RA, Britton KO, Brockerhoff EG, Cavey JF, Garrett LJ, et al. 2014. Effectiveness of the International Phytosanitary Standard ISPM No. 15 on reducing wood borer infestation rates in wood packaging material entering the United States. *PLOS ONE* 9:e96611
61. Haack RA, Petrice TR. 2009. Bark- and wood-borer colonization of logs and lumber after heat treatment to ISPM 15 specifications: the role of residual bark. *J. Econ. Entomol.* 102:1075–84
62. Hajek AE, Diss-Torrance AL, Siegert NW, Liebhold AM. 2021. Inoculative releases and natural spread of the fungal pathogen *Entomophaga maimaiga* (Entomophthorales: Entomophthoraceae) into US populations of gypsy moth, *Lymantria dispar* (Lepidoptera: Erebididae). *Environ. Entomol.* 50:1007–15
63. Hemming V, Burgman MA, Hanea AM, McBride MF, Wintle BC. 2018. A practical guide to structured expert elicitation using the IDEA protocol. *Methods Ecol. Evol.* 9:169–80
64. Hennessey MK, Jeffers L, Nendick D, Glassy K, Floyd L, et al. 2014. Phytosanitary treatments. See Reference 56, pp. 269–308
65. Holmes TP, Allen W, Haight RG, Keskitalo ECH, Marzano M, et al. 2017. Fundamental economic irreversibilities influence policies for enhancing international forest phytosanitary security. *Curr. For. Rep.* 3:244–54
66. Holmes TP, Murphy EA, Bell K, Royle D. 2010. Property-value impacts of hemlock woolly adelgid in residential forests. *For. Sci.* 56:529–40
67. Hope ES, McKenney DW, Pedlar JH, Lawrence K, MacDonald H. 2021. Canadian efforts to slow the spread of emerald ash borer (*Agrilus planipennis* Fairmaire) are economically efficient. *Ecol. Econ.* 188:107126
68. Hoyer-Tomiczek U, Hoch G. 2020. Progress in the use of detection dogs for emerald ash borer monitoring. *Forestry* 93:326–30
69. Hoyer-Tomiczek U, Sauseng G, Hoch G. 2016. Scent detection dogs for the Asian longhorn beetle, *Anoplophora glabripennis*. *EPPO Bull.* 46:148–55
70. Hulme PE. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *J. Appl. Ecol.* 46:10–18
71. Hulme PE. 2014. An introduction to plant biosecurity: past, present and future. See Reference 56, pp. 1–25
72. Hulme PE. 2021. Advancing One Biosecurity to address the pandemic risks of biological invasions. *BioScience* 71:708–21
73. Humble L. 2010. Pest risk analysis and invasion pathways—insects and wood packing revisited: What have we learned? *N. Z. J. For. Sci.* 40:S57–72
74. Int. Plant Prot. Conv. 2021. *Implementation and Capacity Development Meeting (Virtual Meeting N°15)*. Rep., Int. Plant Prot. Conv., Rome. https://assets.ippc.int/static/media/files/publication/en/2021/10/Report_IC_VM15_2021_Jun_2021-08-17.pdf
75. Jactel H, Desprez-Loustau ML, Battisti A, Brockerhoff E, Santini A, et al. 2020. Pathologists and entomologists must join forces against forest pest and pathogen invasions. *NeoBiota* 58:107–27
76. Jamieson LE, Woodberry O, Mascaro S, Meurisse N, Jaksons R, et al. 2022. An Integrated Biosecurity Risk Assessment Model (IBRAM) for evaluating the risk of import pathways for the establishment of invasive species. *Risk Anal.* 42:1325–45
77. Javal M, Roques A, Haran J, Hérard F, Keena M, Roux G. 2019. Complex invasion history of the Asian long-horned beetle: fifteen years after first detection in Europe. *J. Pest Sci.* 92:173–87

78. Kalaris T, Fieselmann D, Magarey R, Colunga-Garcia M, Roda A, et al. 2014. The role of surveillance methods and technologies in plant biosecurity. See Reference 56, pp. 309–37
79. Keller RP, Perrings C. 2011. International policy options for reducing the environmental impacts of invasive species. *BioScience* 61:1005–12
80. Kenis M, Rabitsch W, Auger-Rozenberg MA, Roques A. 2007. How can alien species inventories and interception data help us prevent insect invasions? *Bull. Entomol. Res.* 97:489–502
81. Koch FH, Yemshanov D, Haight RG, MacQuarrie CJ, Liu N, et al. 2020. Optimal invasive species surveillance in the real world: practical advances from research. *Emerg. Top. Life Sci.* 4:513–20
82. Kriticos DJ. 2012. Regional climate-matching to estimate current and future sources of biosecurity threats. *Biol. Invasions* 14:1533–44
83. Kyre BR, Bentz BJ, Rieske LK. 2020. Susceptibility of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) to gene silencing through RNAi provides potential as a novel management tool. *For. Ecol. Manag.* 473:118322
84. Larson ER, Graham BM, Achury R, Coon JJ, Daniels MK, et al. 2020. From eDNA to citizen science: emerging tools for the early detection of invasive species. *Front. Ecol. Environ.* 18:194–202
85. Latombe G, Pyšek P, Jeschke JM, Blackburn TM, Bacher S, et al. 2017. A vision for global monitoring of biological invasions. *Biol. Conserv.* 213:295–308
86. Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proc. R. Soc. B* 269:2407–13
87. Leung B, Roura-Pascual N, Bacher S, Heikkilä J, Brotons L, et al. 2012. TEASIng apart alien species risk assessments: a framework for best practices. *Ecol. Lett.* 15:1475–93
88. Leung B, Springborn MR, Turner JA, Brockerhoff EG. 2014. Pathway-level risk analysis: the net present value of an invasive species policy in the US. *Front. Ecol. Environ.* 12:273–79
89. Liebhold AM, Bascompte J. 2003. The Allee effect, stochastic dynamics and the eradication of alien species. *Ecol. Lett.* 6:133–40
90. Liebhold AM, Berec L, Brockerhoff EG, Epanchin-Niell RS, Hastings A, et al. 2016. Eradication of invading insect populations: from concepts to applications. *Annu. Rev. Entomol.* 61:335–52
91. Liebhold AM, Brockerhoff EG, Garrett LJ, Parke JL, Britton KO. 2012. Live plant imports: the major pathway for forest insect and pathogen invasions of the US. *Front. Ecol. Environ.* 10:135–43
92. Liebhold AM, Brockerhoff EG, Kalisz S, Nuñez MA, Wardle DA, Wingfield MJ. 2017. Biological invasions in forest ecosystems. *Biol. Invasions* 19:3437–58
93. Liebhold AM, Griffin RL. 2016. The legacy of Charles Marlatt and efforts to limit plant pest invasions. *Bull. Entomol. Soc. Am.* 62:218–27
94. Liebhold AM, Kean JM. 2019. Eradication and containment of non-native forest insects: successes and failures. *J. Pest Sci.* 92:83–91
95. Liebhold AM, Leonard D, Marra JL, Pfister SE. 2021. Area-wide management of invading gypsy moth (*Lymantria dispar*) populations in the USA. In *Area-Wide Integrated Pest Management: Development and Field Application*, ed. J Hendrichs, R Pereira, MJB Vreysen, pp. 551–60. Boca Raton, FL: CRC Press
96. Liebhold AM, Tobin PC. 2008. Population ecology of insect invasions and their management. *Annu. Rev. Entomol.* 53:387–408
97. Liebhold AM, Yamanaka T, Roques A, Augustin S, Chown SL, et al. 2016. Global compositional variation among native and non-native regional insect assemblages emphasizes the importance of pathways. *Biol. Invasions* 18:893–905
98. MacLachlan MJ, Liebhold AM, Yamanaka T, Springborn MR. 2021. Hidden patterns of insect establishment risk revealed from two centuries of alien species discoveries. *Sci. Adv.* 7:eabj1012
99. MacLeod A. 2015. The relationship between biosecurity surveillance and risk analysis. In *Biosecurity Surveillance: Quantitative Approaches*, ed. F Jarrad, S Low-Choy, K Mengersen, pp. 109–20. Wallingford, UK: CAB Int.
100. MacLeod A, Pautasso M, Jeger MJ, Haines-Young R. 2010. Evolution of the international regulation of plant pests and challenges for future plant health. *Food Secur.* 2:49–70
101. Madden MJ, Young RG, Brown JW, Miller SE, Frewin AJ, Hanner RH. 2019. Using DNA barcoding to improve invasive pest identification at US ports-of-entry. *PLOS ONE* 14:e0222291

102. Magarey RD, Dolezal WE, Moore TJ. 2010. Worldwide monitoring systems: the need for public and private collaboration. In *Recent Developments in Management of Plant Diseases*, ed. U Gisi, I Chet, ML Gullino, pp. 349–55. Berlin: Springer
103. Marchioro M, Battisti A, Faccoli M. 2020. Light traps in shipping containers: a new tool for the early detection of insect alien species. *J. Econ. Entomol.* 113:1718–24
104. Marzano M, Allen W, Haight RG, Holmes TP, Keskitalo EC, et al. 2017. The role of the social sciences and economics in understanding and informing tree biosecurity policy and planning: a global summary and synthesis. *Biol. Invasions* 19:3317–32
105. Measey J, Visser V, Dgebuadze Y, Li B, Dechoum M, et al. 2019. The world needs BRICS countries to build capacity in invasion science. *PLOS ONE* 17:e3000404
106. Meurisse N, Rassati D, Hurley BP, Brockerhoff EG, Haack RA. 2019. Common pathways by which non-native forest insects move internationally and domestically. *J. Pest Sci.* 92:13–27
107. Morrell JJ. 1995. Importation of unprocessed logs into North America: a review of pest mitigation procedures and their efficacy. *For. Prod. J.* 45:41–50
108. Muirhead JR, Leung B, van Overdijk C, Kelly DW, Nandakumar K, et al. 2006. Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. *Divers. Distrib.* 12:71–79
109. Nahrung HF, Carnegie AJ. 2020. Non-native forest insects and pathogens in Australia: establishment, spread and impact. *Front. For. Glob. Change* 3:37
110. Ormsby M, Brenton-Rule E. 2017. A review of global instruments to combat invasive alien species in forestry. *Biol. Invasions* 19:3355–64
111. Paap T, Burgess TI, Wingfield MJ. 2017. Urban trees: bridge-heads for forest pest invasions and sentinels for early detection. *Biol. Invasions* 19:3515–26
112. Panzavolta T, Bracalini M, Benigno A, Moricca S. 2021. Alien invasive pathogens and pests harming trees, forests, and plantations: pathways, global consequences and management. *Forests* 12:1364
113. Pawson S, Williams N, Gear I, Armstrong J. 2014. Reducing biosecurity business risks for logs and timber. *N. Z. J. For.* 59:22–28
114. Pawson SM, Sullivan JJ, Grant A. 2020. Expanding general surveillance of invasive species by integrating citizens as both observers and identifiers. *J. Pest Sci.* 93:1155–66
115. Perrings C, Burgiel S, Lonsdale M, Mooney H, Williamson M. 2010. International cooperation in the solution to trade-related invasive species risks. *Ann. N. Y. Acad. Sci.* 1195:198–212
116. Piper AM, Batovska J, Cogan NO, Weiss J, Cunningham JP, et al. 2019. Prospects and challenges of implementing DNA metabarcoding for high-throughput insect surveillance. *GigaScience* 8:giz092
117. Poland TM, Rassati D. 2019. Improved biosecurity surveillance of non-native forest insects: a review of current methods. *J. Pest Sci.* 92:37–49
118. Prestemon JP, Turner JA, Buongiorno J, Zhu S, Li R. 2008. Some timber product market and trade implications of an invasive defoliator: the case of Asian *Lymantria* in the United States. *J. For.* 106:409–15
119. Preti M, Verheggen F, Angeli S. 2021. Insect pest monitoring with camera-equipped traps: strengths and limitations. *J. Pest Sci.* 94:203–17
120. Rabaglia RJ, Cognato AI, Hoebeke ER, Johnson CW, LaBonte JR, et al. 2019. Early detection and rapid response: a 10-year summary of the USDA Forest Service program of surveillance for non-native bark and ambrosia beetles. *Am. Entomol.* 65:29–42
121. Rassati D, Faccoli M, Petrucco Toffolo E, Battisti A, Marini L. 2015. Improving the early detection of alien wood-boring beetles in ports and surrounding forests. *J. Appl. Ecol.* 52:50–58
122. Reid CH, Hudgins EJ, Guay JD, Patterson S, Medd AM, et al. 2021. The state of Canada's biosecurity efforts to protect biodiversity from species invasions. *FACETS* 6:1922–54
123. Ricciardi A, Iacarella JC, Aldridge DC, Blackburn TM, Carlton JT, et al. 2021. Four priority areas to advance invasion science in the face of rapid environmental change. *Environ. Rev.* 29:119–41
124. Rihard C, Nguyen R, Brazzel JR. 2019. Pest free areas. In *Quarantine Treatments for Pests of Food Plants*, ed. JL Sharp, GJ Hallman, pp. 213–23. Boca Raton, FL: CRC Press
125. Roe AD, Torson AS, Bilodeau G, Bilodeau P, Blackburn GS, et al. 2019. Biosurveillance of forest insects: part I—integration and application of genomic tools to the surveillance of non-native forest insects. *J. Pest Sci.* 92:51–70

126. Roques A, Shi J, Auger-Rozenberg MA, Ren L, Augustin S, Luo YQ. 2020. Are invasive patterns of non-native insects related to woody plants differing between Europe and China? *Front. For. Glob. Change* 2:91
127. Roy BA, Alexander HM, Davidson J, Campbell FT, Burdon JJ, et al. 2014. Increasing forest loss worldwide from invasive pests requires new trade regulations. *Front Ecol. Environ.* 12:457–65
128. Sarmiento MI, Pint G, Araújo WL, Silva RC, Lima CHO, et al. 2021. Differential development times of galls induced by *Leptocybe invasa* (Hymenoptera: Eulophidae) reveal differences in susceptibility between two *Eucalyptus* clones. *Pest Manag. Sci.* 77:1042–51
129. Schröder ML, Slippers B, Wingfield MJ, Hurley BP. 2020. Invasion history and management of Eucalyptus snout beetles in the *Gonipterus scutellatus* species complex. *J. Pest Sci.* 93:11–25
130. Seebens H, Bacher S, Blackburn TM, Capinha C, Dawson W, et al. 2021. Projecting the continental accumulation of alien species through to 2050. *Glob. Change Biol.* 27:970–82
131. Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, et al. 2017. No saturation in the accumulation of alien species worldwide. *Nat. Commun.* 8:14435
132. Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, et al. 2018. Global rise in emerging alien species results from increased accessibility of new source pools. *PNAS* 115:E2264–73
133. Sharov AA, Liebhold AM. 1998. Bioeconomics of managing the spread of exotic pest species with barrier zones. *Ecol. Appl.* 8:833–45
134. Simberloff D. 2009. The role of propagule pressure in biological invasions. *Annu. Rev. Ecol. Evol. Syst.* 40:81–102
135. Solano A, Rodriguez SL, Greenwood L, Dodds KJ, Coyle DR. 2021. Firewood transport as a vector of forest pest dispersal in North America: a scoping review. *J. Econ. Entomol.* 114:14–23
136. Springborn MR, Lindsay AR, Epanchin-Niell RS. 2016. Harnessing enforcement leverage at the border to minimize biological risk from international live species trade. *J. Econ. Behav. Organ.* 132:98–112
137. Stanaway MA, Zalucki MP, Gillespie PS, Rodriguez CM, Maynard GV. 2001. Pest risk assessment of insects in sea cargo containers. *Aust. J. Entomol.* 40:180–92
138. Suckling DM, Barrington AM, Chhagan A, Stephens AEA, Burnip GM, et al. 2007. Eradication of the Australian painted apple moth *Teia anartoides* in New Zealand: trapping, inherited sterility, and male competitiveness. In *Area-Wide Control of Insect Pests*, ed. MJB Vreyson, AS Robinson, J Hendricks, pp. 603–15. Berlin: Springer
139. Suckling DM, Stringer LD, Baird DB, Kean JM. 2019. Will growing invasive arthropod biodiversity outpace our ability for eradication? *Ecol. Appl.* 29:e01992
140. Suckling DM, Tobin PC, McCullough DG, Herms DA. 2012. Combining tactics to exploit Allee effects for eradication of alien insect populations. *J. Econ. Entomol.* 105:1–13
141. Thompson M, Lyons A, Kumarasinghe L, Peck DR, Kong G, et al. 2011. Remote microscopy: a success story in Australian and New Zealand plant biosecurity. *Aust. J. Entomol.* 50:1–6
142. Tobin PC, Blackburn LM. 2007. *Slow the spread: a national program to manage the gypsy moth*. Gen. Tech. Rep. NRS-6, North. Res. Stn., For. Serv., US Dept. Agric., Madison, WI
143. Tobin PC, Kean JM, Suckling DM, McCullough DG, Herms DA, Stringer LD. 2014. Determinants of successful arthropod eradication programs. *Biol. Invasions* 16:401–14
144. Turner RM, Brockerhoff EG, Bertelsmeier C, Blake RE, Caton B, et al. 2021. Worldwide border interceptions provide a window into human-mediated global insect movement. *Ecol. Appl.* 31:e02412
145. US Dept. Agric. 2021. Removal of emerald ash borer domestic quarantine regulations. *Fed. Regist.* 85:81085–95
146. US Dept. Agric. 2022. *Lymantria dispar Digest 2.1.01*. Database, For. Serv., US Dept. Agric., Washington, DC, updated Jan. 12. <https://apps.fs.usda.gov/nicportal/lddigest/cfm/dsp/dspSuppressionCostByYearForProgram.cfm>
147. Valentin RE, Fonseca DM, Gable S, Kyle KE, Hamilton GC, et al. 2020. Moving eDNA surveys onto land: strategies for active eDNA aggregation to detect invasive forest insects. *Mol. Ecol. Res.* 20:746–55
148. Van Rooyen E, Paap T, De Beer ZW, Townsend G, Fell S, et al. 2021. The polyphagous shot hole borer beetle: current status of a perfect invader in South Africa. *S. Afr. J. Sci.* 117:9736
149. Venette RC. 2017. Climate analyses to assess risks from invasive forest insects: simple matching to advanced models. *Curr. For. Rep.* 3:255–68

150. Ward SF, Fe S, Liebhold AM. 2019. Spatial patterns of discovery points and invasion hotspots of non-native forest pests. *Glob. Ecol. Biogeogr.* 28:1749–62
151. Welsh MJ, Turner JA, Epanchin-Niell RS, Monge JJ, Soliman T, et al. 2021. Approaches for estimating benefits and costs of interventions in plant biosecurity across invasion phases. *Ecol. Appl.* 31:e02319
152. Whattam M, Clover G, Firko M, Kalaris T. 2014. The biosecurity continuum and trade: border operations. See Reference 56, pp. 269–308
153. Wilson AD, Forse LB, Babst BA, Bataineh MM. 2019. Detection of emerald ash borer infestations in living green ash by noninvasive electronic-nose analysis of wood volatiles. *Biosensors* 9:123
154. Withers TM. 2001. Colonization of eucalypts in New Zealand by Australian insects. *Austral Ecol.* 26:467–76
155. Yamanaka T, Liebhold AM. 2009. Spatially implicit approaches to understand the manipulation of mating success for insect invasion management. *Popul. Ecol.* 51:427–44
156. Yemshanov D, Haight RG, MacQuarrie CJ, Koch FH, Liu N, et al. 2020. Optimal planning of multi-day invasive species surveillance campaigns. *Ecol. Solut. Evid.* 1:e12029
157. Zahid MI, Grgurinovic CA, Walsh DJ. 2008. Quarantine risks associated with solid wood packaging materials receiving ISPM 15 treatments. *Aust. For.* 71:287–93
158. Zahrnt V. 2011. Transparency of complex regulation: How should WTO trade policy reviews deal with sanitary and phytosanitary policies? *World Trade Rev.* 10:217–47