Invasions of non-native forest insects and pathogens continue despite ongoing countermeasures by federal and state agencies; on average, 2.5 previously unrecognized non-native insect species establish per year in the US (Aukema et al. 2010). Damages from these forest invaders cost US taxpayers several billions of dollars annually (Pimentel et al. 2005; Aukema et al. 2011). These costs are borne in part by federal, state, and local governments, which work to eradicate newly established pest populations, to slow the spread of established pests, and to remove hazardous dead trees on public lands. But major costs are also assumed by landowners who may lose valuable forest resources, as well as by homeowners who often must pay large sums for tree removal/replacement and suffer losses in property value resulting from associated tree mortality (Aukema et al. 2011). Less is known about the effects of invasive species on ecosystem services, although some pest invasions (e.g., chestnut blight in North America) have virtually extirpated their host tree species; thus, cascading environmental impacts may be substantial.

The importance of the plant trade as an invasion pathway for arthropod pests in Europe was recognized in several previous studies. By analyzing the non-native insect fauna in Switzerland and Austria and assessing the most likely introduction pathway for each species, Kenis et al. (2007) estimated that at least 43% of these introductions were the result of the plant trade, mainly that of ornamentals (including cut flowers). Expanding this analysis to all established non-native arthropods in Europe, Roques et al. (2009) attributed 38% of introductions to the horticultural and ornamental trade (including cut flowers and seed). Likewise, Smith et al. (2007) attributed nearly 90% of “human-assisted” invertebrate pest introductions in the UK between 1970 and 2004 to the plant trade. Live plants are also an important pathway for invasive plant pathogens, which are particularly difficult to detect in port inspections (Palm and Rossman 2003; Rossman 2009).

Here, we provide the first report quantifying the role of the live plant pathway for invasions of forest insect pests and diseases that have become established in the US. We also use historical trade data to characterize temporal trends in live plant imports, as well as historical pest interception data to illustrate the efficacy of plant import inspection stations. In this analysis, we include all live plants intended for retail and propagative use. In addition to including plants with roots, this commodity category also referred to as “plants for planting” or “nursery stock” – encompasses bulbs, roots, and unrooted cuttings, but excludes cut flowers, ornamental foliage, and seed.

### Forest pest invasion pathways

Of 455 species of non-indigenous forest insects and diseases documented in the US (Aukema et al. 2010), 82...
Figure 1. Most likely pathways for forest pathogens and different insect guilds. Pathway assignment for individual species was based on published information and biology, as detailed in WebTables 1–4.

(representing 65 insects and 17 pathogens) were designated as having “high impact” (based on at least one published report of associated damage to forest tree species). For each of these 82 species, we identified the most likely pathway by which their invasion occurred, in most cases by relying on previous publications either reporting their invasion history or identifying that pathway given the species’ biology. In instances where publications indicating a likely pathway were lacking, we designated the most likely pathway based upon species’ biological characteristics and/or historical interceptions at ports-of-entry. Other possible pathways were also specified (WebTables 1–4).

The most common invasion pathway into the US for damaging forest insects and pathogens is via live plants (Figure 1), with approximately 69% of established, damaging non-native forest pests attributed to the live plant trade (Panel 1, a–d). This value is intermediate compared with previous estimates for Europe (Kenis et al. 2007; Smith et al. 2007; Roques et al. 2009). Although similar to methods used previously, our pathway analysis was limited to forest pests, and only to those that cause substantial impacts. Smith et al. (2007) attributed a much higher percentage of pests in the UK to the plant trade. Though it is tempting to suggest that this outcome is due to the historical predilection of the British people for collecting exotic plants, note that the analysis by Smith et al. (2007) examined all pest establishments in the UK in the recent past. In contrast, our analysis reported here did not limit the time of introduction. While the rate of accumulation of forest pests in general has been relatively constant since 1860 (Aukema et al. 2010), changes in trade and phytosanitary practices have likely altered the relative importance of particular pathways. For example, Aukema et al. (2010) found that establishment of wood-borers increased faster than any other insect guild since the 1980s, and attributed this to the increased volume of containerized freight and accompanying wood packaging material.

The most common pathway also varied considerably among insect guilds (Figure 1). A total of 95% of sap-feeding insects and 89% of foliage-feeding insects most likely entered the US on live plants (WebTables 1 and 2),
but most wood- and phloem-boring insects (borers) likely entered the country on wood packaging materials, as well as logs, lumber, or other wood sources (87.5%). Only 12.5% of borers (the most costly insect guild; Aukema et al. 2011) are believed to have entered via live plants (WebTable 3). For forest pathogens, 47% are attributed to the live plant pathway and 19% of invasions were associated with trade in wood (WebTable 4).

- Characterizing the US international plant trade

The quantity of plant imports rose substantially during the past 43 years (US Department of Commerce 2011), increasing by more than 500% (an average increase of 51 million plants per year) to a maximum of 3.15 billion plants in 2007 (Figure 2). The recent economic downturn may account for the decline in plant imports during calendar years 2008 and 2009.

Since 1967, the value of all imported plants increased from nearly $94 million to a high of $647 million in 2004 (Figure 2; unless otherwise indicated, all monetary values reported in the text are in US$). Between 1989 and 2002, the value share of imported plants annually averaged only 3.1% of domestic consumption. The value of US nursery plant exports was substantially less, averaging $206.5 million annually (2005–2007). Dracaena was the genus most frequently imported between 2005 and 2009, followed by Verbena, Calibrachoa, Codiaeum, Petunia, Phalaenopsis, Impatiens, Osteospermum, Lantana, and Lobelia; imported plants belonging to these genera tended to be tropical in origin, meant for indoor use, or destined for ornamental bedding. After imported plants cleared the inspection process at their respective ports-of-entry (see section below), their destinations were California (27%), Florida (19%), Illinois (7%), Ohio (6%), New Jersey (6%), New York (6%), Michigan (4%), Colorado (3%), Pennsylvania (3%), and all other states combined (19%).

Woody ornamentals are more likely than herbaceous plants to harbor forest pests, and the probability of pest establishment may be elevated when the former are planted outdoors, in close proximity to other live hosts (Smith et al. 2007). During 1996–2009, an average of 105 million live trees and shrubs were imported to the US. The changing demographics of shipment origins for woody plants (WebTable 5) are revealed by contrasting the average volume of imported plants and market share between 1989 and 1993 with imports between 2005 and 2009. Canada is the listed source of 97% of woody plants, although Asia and Oceania are the fastest growing sources. Between 2005 and 2009, nearly 135 million plants on

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average were imported annually with soil or potting media attached to roots, which increases the risk of transferring soil-borne insects and pathogens, with 94% of such plant shipments originating in Canada (WebTable 6).

**Plant shipment inspections and the pests they find**

The US Department of Agriculture's (USDA's) Animal and Plant Health Inspection Service (APHIS) inspects imports of plants, cuttings, and seeds, all of which must arrive at one of 17 Plant Inspection Stations located at ports-of-entry throughout the US. Activities at these stations include the physical inspection of plant material, identification of plants, seeds, and pests, and application of disinfection treatments. The Plant Inspection Stations also issue federal phytosanitary certificates (documents certifying the absence of regulated pests or confirming a treatment required by the importing country) for exports. In all, approximately 65 full-time personnel are employed to inspect incoming plant shipments (Figure 3), leading to an average workload in fiscal year (FY) 2010 of 43 million plants per inspector. Data on shipments inspected and pests detected are maintained by APHIS.

During FY 2003–2010, 22,267 shipments – representing 2.6% of the total number of incoming shipments – were found to be infested with at least one “reportable” pest species in normal port-of-entry inspections. Indeed, many of these shipments were found to contain more than one pest species. By examining records stored in the APHIS Pest Interception Database (PestID) (McCullough et al. 2006), we were able to characterize the types of detected pest species.

Most intercepted pests (18,008) were insects (Figure 4a), predominated by the Order Homoptera – sucking insects, which include most insect vectors of plant viruses (Figure 4b). Among the non-insect pests, mites were detected in 6,210 shipments, diseases in 2,773 shipments, mollusks in 2,187 shipments, nematodes in 81 shipments, and noxious weeds in 360 shipments (Figure 4a).

**Inspection efficacy**

In addition to conducting standard port inspections, APHIS implements the Agriculture Quarantine Inspection Monitoring (AQIM) program to monitor the effectiveness of these inspections and to provide a scientific basis for improving inspection procedures. Under AQIM, passenger baggage, vehicles, mail, and cargo are randomly sampled at seven of the 17 Plant Inspection Stations and undergo more thorough inspection processes to produce statistically based estimates of approach rates (percent of inspected shipments that are found to be infested) for potential pests (Work et al. 2005). Since 2008, live plant shipments have been included in the AQIM program; specifically, randomly selected shipments of live plants belonging to 24 commonly imported genera were subject to the more thorough AQIM inspection process. To determine inspection efficacy of the Plant Inspection Stations’ normal operating procedures, we compared FY 2009 records of pest interceptions from AQIM sampling of plant propagative materials in cargo with the interception rate over the same period for shipments of the same 24 plant genera from PestID. Because the AQIM inspection methods are more thorough, it is reasonable to assume that the AQIM results provide a more accurate estimate of the actual infestation rate.

Under standard port inspections, infestations were detected in 810 out of 24,781 total recorded shipments (equivalent to 3.3%) of the 24 plant genera. In contrast, in a random subsample of inspections under the more thorough AQIM process conducted by the same inspectors, 118 out of 996 shipments (equivalent to 11.9%) were found to contain reportable pests. Conservatively
assuming that AQIM results reflect the actual infestation rate, then approximately 8.6% (ie the difference in infestations between AQIM inspections and standard inspections) of all incoming shipments were infested but escaped detection under standard inspection procedures. Expressed another way, only 28% of actual infestations were detected by standard inspections, whereas 72% escaped detection.

Even the most thorough port inspections are unlikely to detect all arriving pests, because some infestations will not display easily recognizable signs or symptoms of pests at the moment of passage. Therefore, if 11.9% of shipments were visibly infested, the actual infestation rate was probably higher. The total number of individuals of a species arriving per unit time – “arrival rate” (Brockerhoff et al. 2006) or “propagule pressure” (Lockwood et al. 2005; Von Holle and Simberloff 2005) – strongly influences the establishment success of non-native species, and thus it is important to reduce the arrival rate to mitigate future invasions.

Regulation of live plant imports: outdated assumptions

Regulation of live plant imports by the USDA is codified in Title 7 of the Code of Federal Regulations, Part 319, Section 37 (“Nursery Stock, Plants, Roots, Bulbs, Seeds, and other Plant Products”). This regulation, also known as “Quarantine 37”, was promulgated in 1918 “to reduce to the utmost the risk of introducing plant pests with plant importations” (Weber 1930). The regulatory design of the quarantine was based on existing conditions and particular assumptions. At the time, it was assumed that (1) typical shipments would be small (fewer than 100 individual plants) and infrequent; (2) imports would mainly be for the establishment of domestic propagation
Stock and not for direct resale; (3) mandatory fumigation with methyl bromide would be applied to exterminate arthropod pests; (4) imports would enter only through ports with specialized staff and inspection facilities; and (5) taxa known to carry pests that are difficult to detect (e.g., pathogens) would be prohibited or have special requirements. These conditions prevailed until the 1970s (USDA-APHIS 2004).

Despite the recognized necessity for trade restrictions on certain plants to mitigate the introduction of harmful non-native pests, the counteracting need to import new plant species and varieties – to increase the germplasm available to US growers – was a powerful influence on subsequent changes to Quarantine 37. The horticulture industry favored a regulatory design that encouraged exploration of plant taxa for agriculture- and especially horticulture-based applications. At the time, however, there was limited understanding of the invasive potential of certain plants or of the risk magnitude posed by pests in the trade of propagative material. In addition, favorable growing conditions and inexpensive labor overseas led the industry to import large amounts of plants for domestic planting, or for immediate sale to consumers (USDA-APHIS 2004).

Today, US plant import regulations categorize imported plants as either prohibited (not allowed) or restricted (allowed under certain conditions). Specifying prohibited plants and allowing entry to the unspecified remaining genera is referred to as a “black list” approach. Most plant genera are permitted entry if accompanied by a phytosanitary certificate from the country of origin and inspected upon arrival at a Plant Inspection Station.

Some plant genera are required to be held in post-entry quarantine for specific time periods. There are no longer mandatory fumigation requirements for all plants, and no limits on shipment size; some shipments now consist of hundreds of thousands of plants.

To address concerns about the influx of pests via live plants, APHIS recently established a new “gray list” category of live plants – those “Not Approved Pending a Pest Risk Analysis” (NAPPRA; USDA-APHIS 2011a). Instituted in 2011, NAPPRA includes two lists: (1) potential quarantine pest plants (i.e., weeds) and (2) potential hosts of quarantine pests. Initially, the gray list will focus on plants that have not been imported in large quantities in the past; for example, several forest tree genera have been proposed for inclusion in the NAPPRA category. This new category allows APHIS to respond more quickly to scientific evidence demonstrating that a plant taxon is itself a pest, or may carry a pest of concern, without first engaging in a lengthy pest risk analysis. APHIS accepts public input for plant taxa that should be listed in this category (www.aphis.usda.gov/import_export/plants/plant_imports/Q37/nappra/suggestions.shtml), and contributions from the scientific community could greatly enhance the protection of natural resources through this important tool.

Although there are no data to empirically evaluate the role of plant smuggling in the introduction of insect pests and diseases, there are several instances where pests have arrived despite regulations prohibiting host entry; plant smuggling may be the most likely explanation for these cases. For example, the chestnut gall wasp (Dryocosmus kuriphilus), a harmless insect in its native range in China, was found in 1940 in Japan and in 1974 in the US, where it was illegally imported on smuggled budwood (Rieske 2007). It has become the most severe insect pest of American chestnut (Castanea dentata) and

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**Panel 1d. Examples of forest pests introduced via live plants**

**Light brown apple moth (Epiphyas postvittana)**
The Australian light brown apple moth (LBAM; Epiphyas postvittana) is a highly polyphagous pest, affecting many trees (horticultural and otherwise) and other plants (Suckling and Brockerhoff 2010). LBAM was accidentally introduced to New Zealand, Hawaii, and the UK, and it has been intercepted numerous times at US and New Zealand borders and in several other countries on fruit and live plants (e.g., Venette et al. 2003; New Zealand Ministry of Agriculture and Forestry 2011). In 2006, two LBAM were found in Berkeley, California. Subsequent delimitation trapping and trace-backs of finds on nursery plants revealed the presence of the largest populations around Santa Cruz, California, where the California Department of Food and Agriculture detected heavy infestations in several wholesale nurseries. Some of these nurseries had imported nursery stock from Australia and New Zealand, suggesting that the initial introduction may have occurred there. Though importation of cut flowers and fresh produce represent alternative pathways by which the species could have possibly gained entrance, various evidence supports live plant importation as the most likely entry pathway.

An economic risk analysis suggested that damages to California’s four main fruit crops, as well as quarantine and other costs, could reach $105 million annually (Fowler et al. 2007). Although the moth’s California distribution in 2007 spanned approximately 150-km north–south and 40-km inland, eradication efforts were undertaken because of the potential damage and impacts on trade (Suckling and Brockerhoff 2010). In 2008, the USDA’s budget for the eradication was $74.5 million. However, further spread of LBAM occurred, probably aided by long-distance movements of nursery plants and infested crops; the program goal was eventually changed from moth eradication to containment.
New horizons in regulating the plant trade

In further efforts to address the live plant invasion pathway, the North American Plant Protection Organization adopted Regional Standard for Phytosanitary Measures number 24 in 2005 (NAPPO 2005), signaling the intention of the three member countries (Canada, the US, and Mexico) to develop and implement regulations that rely on an integrated measures approach to pest risk management in live plants. This approach has the advantage of reducing unknown as well as known pest problems through the use of best management practices at plant nurseries, although required measures must be based on specific pest risks. The process of developing and implementing regulations for integrated measures is complicated by the myriad of host plants and potential pests for which appropriate pest risk management measures must be determined and negotiated between trading partners.

Both APHIS and the Canadian Food Inspection Agency are testing a pilot nursery certification program that uses an integrated measures approach to address particular pests on specific plants from specific geographical locations. A participating facility must maintain records that verify the origin of all plant material and document the required monitoring and production practices. The facility must also ensure that only eligible plant material is exported under the program. After participating in the program for 1 year, the facility then becomes eligible to issue its own phytosanitary certificate, thus expediting shipping and passage through ports and reducing the chances of shipment rejection.

Similar “pre-clearance” programs exist for bulbs from the Netherlands. Pre-clearance programs expedite trade because entry requirements are met in the country of origin. Such programs may be more effective at pest detection than port inspections because the former often require growing-season inspections that facilitate detection (if pests are present), whereas plant material is often shipped and thus inspected in a dormant state (in which pests may be more difficult to detect). Industry benefits from faster access to markets, which results in fresher products, as well as reduced rejection rates and arrival delays. Rejections are also less costly when imposed prior to shipping.

The International Plant Protection Convention (IPPC) is working to standardize an integrated measures approach to reduce pest presence in the live plant trade (IPPC 2006). Our findings support the need for more robust methods to maintain and verify plant health. Clearly, given the volume of current trade in live plants and the difficulties of detecting pests in ports, we should seek methods that complement inspection and provide more comprehensive approaches to manage pest-related risks. Combined improvements will minimize the likelihood of introducing non-native pests via live plants.

Conclusions

Live plants represent the most common pathway by which non-native forest insects and pathogens have likely arrived in the US. Furthermore, international movement of plants is increasing worldwide, as demonstrated by the data presented here on live plant imports to, and exports from, the US. While live plants were previously introduced to the US mainly for plant breeding purposes and as propagation stock, there is a rapidly increasing trend in large volumes of plants being grown overseas for domestic planting or US retail sales. Given this trend, non-native forest insect and pathogen invasions may likely increase in the future under the current system; thus, it is important to address this anticipated and developing invasion pathway. Bradley et al. (2012) recently discussed trends of increasing plant imports relative to the risks of novel plant invasions, but here we identify perhaps an even more insidious problem of plant pests associated with plant imports.

One mitigation approach would be to intensify inspection efforts at Plant Inspection Stations. Although not all actionable pests found by inspectors at any level of inspection pose the same risk to US plant resources, there are nevertheless practical limitations to our ability to detect pests as they pass through ports. To avoid prohibitively expensive increases in personnel and facilities, APHIS recently announced the implementation of a risk-based inspection process that will target shipments of high-risk plants for more intense inspections, recognizing that it is impractical to completely inspect every item (USDA-APHIS 2011b). Molecular technology should be explored to improve detection – especially for plant pathogens, which are particularly difficult to detect visually.

Another alternative would be to adopt a “white list” system, such as that used in Australia. Australian regulations prohibit plants from entry until a pest risk assessment demonstrates that they pose very little risk. Most of the species for which entry is approved also require a post-entry quarantine. The Australian system has been shown to produce net bioeconomic benefits (Keller et al. 2007).

Other countries, such as New Zealand, require post-entry quarantine of all imported whole plants and cuttings. In the US, post-entry quarantine is required for certain genera of plants; for example, grapevines and fruit trees are imported into a post-entry quarantine program called the National Clean Plant Network (NCPN), under which incoming germplasm is screened for pathogens and maintained as a source of pathogen-free propagative material for industry. Expanding NCPN to include ornamental plants would be an expensive, but probably effective, option.

Smuggling of plant germplasm may increase with trade restrictions. Rigorous enforcement of regulations will need to be coupled with aggressive consumer/importer education programs that highlight the importance of compliance to protect natural resources.
There is, moreover, an intrinsic weakness in any system that relies on knowing what pests exist on ornamental crops in the country of origin, because such background knowledge is not robust (Simberloff 2000, 2001; Reaser et al. 2008). This difficulty plagues both “black list” and “white list” countries. One widely respected and outspoken critic points out that pests that coevolved with hosts in the country of origin are unlikely to be damaging enough there to allow experts to predict their risk in novel ecosystems and hosts (Brasier 2008).

Although reducing the lag time to limit introductions once pest threats are recognized, the new NAPPRA category still depends on advance knowledge of existing pest threats. Yet most microorganisms are as yet unknown to science. In 2009 alone, 6129 unique combinations of “country of origin” and “plant genus” were imported into the US. Such a diversity of plant imports increases the introduction likelihood of potential pests and diseases that these plants might harbor. Expansion of offshore information gathering, through systems such as APHIS Offshore Pest Information Program and the Sentinel Plant Network, which could collect data on pests of plants native to the US that are growing abroad, would help inform list-based systems.

The integrated systems approach called for by the North American Plant Protection Organization standard, and being explored by the IPPC, offers the potential to address this unknown diversity of pests. However, expanded partnerships between the research community and the nursery industry are needed to develop best management practices that provide affordable and broadly effective pest management systems.

Further research is necessary to evaluate the costs and benefits of various approaches to reducing pest risk in live plant imports. However, it is unrealistic to expect any single approach to solve the problem of pest imports via the plant trade pathway. A holistic system, relying on improvements in offshore production practices, plant-tracking systems, risk-based inspection procedures, and more effective phytosanitary practices in receiving nurseries, would be more likely to reduce risks to an acceptable level.

As global trade expands, our knowledge of pest pathways must be improved to ensure trade is accomplished with minimal environmental degradation. Agricultural quarantine inspection monitoring surveys, such as AQIM, can provide very useful information on the efficacy of current practices, as demonstrated here. Such robust sampling of other high-risk commodities can inform prevention activities to address other critical pest pathways, such as wood packaging materials.

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