Historical Accumulation of Nonindigenous Forest Pests in the Continental United States

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Nonindigenous forest insects and pathogens affect a range of ecosystems, industries, and property owners in the United States. Evaluating temporal patterns in the accumulation of these nonindigenous forest pests can inform regulatory and policy decisions. We compiled a comprehensive species list to assess the accumulation rates of nonindigenous forest insects and pathogens established in the United States. More than 450 nonindigenous insects and at least 16 pathogens have colonized forest and urban trees since European settlement. Approximately 2.5 established nonindigenous forest insects per year were detected in the United States between 1860 and 2006. At least 14% of these insects and all 16 pathogens have caused notable damage to trees. Although sap feeders and foliage feeders dominated the comprehensive list, phloem- and wood-boring insects and foliage feeders were often more damaging than expected. Detections of insects that feed on phloem or wood have increased markedly in recent years.

Keywords: invasive pests, forest insects, forest pathogens, feeding guild, detection rates

Nonindigenous insects and pathogens pose a significant threat to the productivity and diversity of forest ecosystems in the United States (Liebhold et al. 1995, Wilcove et al. 1998, Simberloff 2000, Allen and Humble 2002). Awareness of the ecological and economic impacts associated with introduced insects and pathogens (hereafter, pests) has increased in recent years, in part because of highly damaging pests such as the Asian longhorned beetle (*Anoplophora glabripennis* [Motschulsky]), emerald ash borer (*Agrilus planipennis* Fairmaire), and sudden oak death (*Phytophthora ramorum* Werres, De Cock & Man in't Veld) (Nowak et al. 2001, Rizzo and Garbelotto 2003, Cappaert et al. 2005). Unintentional introductions of nonindigenous species are typically by-products of economic activity. Phytophagous (plant-feeding) insects and plant pathogens may be transported inadvertently with their hosts when nursery stock, produce, or related commodities are shipped. Additional introductions occur when species hitchhike on commodities that may or may not include their host plants (Levine and D'Antonio 2003, Work et al. 2005, McCullough et al. 2006, Westphal et al. 2008). Fortunately, only a fraction of species that arrive in a new environment become established, and an even smaller proportion become invasive pests (Williamson and Fitter 1996).

Along with other countries, the United States has implemented regulations designed to reduce the rate of introductions of nonindigenous plant-feeding insects and plant pathogens, beginning with the Plant Quarantine Act (1912). Subsequent regulatory efforts arose from the Organic Act (1944), the International Plant Protection Convention (1952), the Federal Plant Pest Act (1957), the National Environmental Policy Act (1970), and the Plant Protection Act (2000). Within the United States, federal or state quarantines, inspections, and other regulatory efforts are often imposed to limit the transport of established invasive insects and plant pathogens into new regions.

Temporal patterns of introductions

As a result of rapidly increasing global trade and travel, one might expect a concurrent trend of rising rates of nonindigenous species establishment (Levine and D'Antonio 2003). Indeed, patterns of acceleration in cumulative numbers of establishments have been documented in a variety of taxonomic groups (Wonham and Pachepsky 2006), but such temporal trends have never been demonstrated for forest pests. We investigated whether the rate of accumulation of nonindigenous forest pests in the continental United States has (a) accelerated with increases in international trade and travel during recent decades, (b) remained steady, or (c) decreased as a result of more stringent regulatory measures. Nonindigenous organisms have been introduced both intentionally and accidentally since Europeans first arrived in North America in the 1500s (Levine and D'Antonio 2003, Westphal et al. 2008). More than 400 insect species native to Europe feed on trees, shrubs, or other woody vegetation in North America (Matern et al. 2002, Mattson et al. 2007,

Langor et al. 2009). The predominance of alien insects of European origin probably reflects the long history of trade, immigration, and travel between Europe and North America, as well as similarities between the vegetation and climates of these regions (Niemela and Mattson 1996, Langor et al. 2009). Additionally, because of frequent disturbances in their native habitats, selection may have favored European insect species with traits conducive to the successful colonization of new habitats (Sailer 1983, Mattson et al. 2007).

In the past 25 years, trade between the United States and other regions of the world, including Asia, Central America, and South America, has increased substantially, providing unprecedented opportunities for inadvertent introductions of organisms native to these regions (Levine and D'Antonio 2003, McCullough et al. 2006). The Asian longhorned beetle; the emerald ash borer; and the redbay ambrosia beetle (*Xyleborus glabratus* Eichhoff), which is the vector of laurel wilt disease (*Raffaelea lauricola*), are examples of insects native to Asia that probably arrived in the United States in the 1990s (Haack et al. 1997, Siegert et al. 2007, Koch and Smith 2008). Resources and regulatory efforts directed at stemming the burgeoning tide of potentially damaging forest pest introductions have been criticized as inadequate (GAO 1997, 2006, Simberloff et al. 2005, Work et al. 2005, Reaser and Waugh 2007). However, the long-term economic benefits to countries that apply risk-assessment technologies to identify and exclude potentially destructive invasive species are potentially large (Keller et al. 2007). Policymakers, however, must weigh the trade-offs associated with the impacts of invasive forest pests with the consequences of regulatory action. When a new, damaging pest is discovered, regulatory actions can have serious consequences for plant-related industries in affected areas. Policies may mandate inspections or pesticide applications, increasing production costs and potentially negating opportunities for successful implementation of biological control for native pests, as well as perhaps causing other adverse environmental impacts. In some cases, the transport of nursery stock, logs, or related products may be severely restricted, limiting the viability of businesses affected by the regulations.

A greater understanding of the accumulation of nonindigenous insects and pathogens could inform decisions by policymakers, regulatory officials, and resource managers charged with exclusion, detection, or management of invasive species in US forests. We compiled a list of established, nonindigenous forest insect and pathogen species in the United States, and we recorded the year each species was first detected (when known) and identified species that cause measurable damage. We assigned insects to feeding guilds for additional analyses. Using these data, we calculated the rate of accumulation of nonindigenous pests in US forests and how patterns of accumulation varied over time and among insect feeding guilds.

List of established insect pests
We assembled a list of nonindigenous insects known to colonize forest trees with at least one recorded location of establishment in the continental United States (available at

http://knb.ecoinformatics.org/knb/metacat/nuding.7.6/knb). We based our list on published lists and reports (Mattson et al. 1994, 2007, Haack 2006, Langor et al. 2009) and communications with experts. Species included in our list had to feed on at least one tree species found in native forests or common in urban forest settings (e.g., *Eucalyptus*). We excluded species that have gradually expanded their ranges continuously as a result of migration or climate change, and indigenous invaders (i.e., species native to the United States but introduced into previously uncolonized US regions). We excluded insects and pathogens that colonize primarily agricultural commodities, shrubs, herbaceous plants, and dead or processed wood, as well as predatory, parasitic, and aquatic insects, detritivores, pollinators, and those insects that feed on trees only occasionally.

For each insect species on our list, we recorded taxonomy (order, family, genus, species), year or approximate year the species was detected or identified in the United States (when known), feeding guild, and primary host species (when available). For the family Curculionidae, we distinguished between the subfamily Scolytinae, which includes bark and ambrosia beetles, and other curculionids (weevils) for some analyses because of differences among these groups in behavior, survey efforts, and potential impacts. Insects in the order Hemiptera were grouped by suborder for some analyses, when we wished to distinguish among Prosorrhyncha (true bugs), Clypeorrhyncha (leafhoppers, froghoppers), and Sternorrhyncha (aphids, adelgids, scales, whiteflies).

When the date of detection for a given species was approximate, we used the following guidelines for analysis: approximately 1950 = 1950; earlier than 1950 = 1949; 1950s = 1955; 1800s = 1850. When more than one date was reported, we used the earliest date for analysis (e.g., 1950 and 1956 = 1950). In some cases, the detection date was noted as occurring in the "early," "mid," or "late" portions of the 19th or 20th centuries; for these species, we divided the century into thirds and used the midpoint for analysis. For example, 1816, 1850, or 1883 were used for species first identified in the early, mid, or late 1800s, respectively. Similarly, we assigned dates to species first identified in the early, mid, or late portion of a given decade. For example, 1922, 1925, or 1928 were used for pests first identified in the early, mid, or late 1920s, respectively. Although we used the earliest date of detection for our analyses, we recognize that lag times are inherent in these records.

We assigned insect species to feeding guilds on the basis of their dominant or most-damaging feeding mode. Although insect feeding habits vary among orders and even among families, if we had created numerous guilds, each composed of relatively few species, it would have severely limited our ability to evaluate temporal trends. Foliage feeders included insects that feed externally or internally on leaf or needle tissue. A few insects that feed on meristematic tissue in apical or lateral shoots were included in the foliage-feeding guild because the damage associated with these species (e.g., loss of leaf area, topkill, or loss of

apical dominance) is similar to that caused by many foliage-feeding insects. Sap feeders included gall-forming adelgids, as well as insects such as scales, aphids, psyllids, and white-flies. The phloem- and wood-borer guild included species that feed aboveground on phloem, cambium, or wood. We assigned species that feed primarily on roots, seeds, cones, or fruit to the "other" guild. We assigned insect species that feed on different plant tissues as juveniles and adults to the feeding guild most associated with injury or damage. For example, we assigned the emerald ash borer to the phloem- and wood-borer guild because phloem feeding by larvae causes tree mortality, whereas foliage feeding by adult beetles causes negligible injury.

We also included host breadth of each species in our list, following the classifications of Niemela and Mattson (1996). Insect species that feed on a single genus of host plants were considered monophagous, whereas we recorded species that feed on multiple genera of a single plant family as oligophagous. Species that feed on hosts representing multiple plant families were considered polyphagous.

List of high-impact insects

We identified a subset of insect species from the original list that included species of regulatory significance and species reported to have a significant (above background levels) impact on live trees in some areas of the United States. Impacts included tree mortality (including seedlings), canopy thinning or dieback (branch death), growth loss, defoliation, decreased reproduction or regeneration (e.g., seed or cone damage), or other ecological or aesthetic effects in forest or urban trees. We excluded pests that cause economic damage only to commercial fruit orchards. At least one published report of damage was required before a species could be included on the high-impact list. Primary host species were identified for each species on the high-impact list. We excluded secondary hosts, hosts that are rarely colonized, or hosts colonized only in experimental conditions. Our sources of information included scientific journals, regulatory reports, and university extension publications.

List of high-impact pathogens

We also included pathogens affecting live trees on the high-impact list. We could not compile a list of nondamaging pathogens comparable to our long list of insects because new introductions of fungi and other microorganisms are rarely detected and identified if they cause no damage. We used the same criteria, including a reported impact affecting at least one tree host, to identify pathogens for inclusion on the high-impact list and we recorded the same variables for pathogens and insects.

Statistical methods

The relationship between the cumulative number of detected establishments of nonindigenous insects and time is well described by a linear function from 1860 to 2006

(figure 1; $r^2 = 0.988$); therefore, we used this time period for further analyses. Because detection dates were unknown for many insect species, we report a minimum and maximum accumulation rate. To calculate the minimum rate, we determined the average number of species per year known to have been detected between 1860 and 2006. We estimated the maximum accumulation rate by including all species detected within this time period, as well as all the species of unknown detection date. To determine whether the unknown dates were evenly distributed among guilds and to assess whether there was any difference in the probability that insects from particular guilds, orders, or host breadth became damaging pests on the high-impact list, we used Fisher's exact and Pearson's χ^2 tests, and calculated p values using a Monte Carlo test with 100,000 replicates. We used similar methods to assess the accumulation rate from 1860 to 2006 for insects and pathogens on the high-impact list.

We applied Poisson regression from the family of generalized linear models (McCulloch and Searle 2001) to evaluate the number of nonindigenous insects identified over time by feeding guild (phloem and wood borers, foliage feeders, sap feeders, and other). The response is a ratio with a numerator equal to the summed counts over the time periods from 1635 to 1739 (115 years), from 1740 to 1849 (110 years), then every 10 years until 1999 (10 years), and then from 2000 to 2006 (7 years); the denominator is equal to the length of the described time periods divided by 10. This resulted in 18 10-year time units and 67 ratios (number of species in 10 years). The summed counts (ratios' numerator) were assumed to
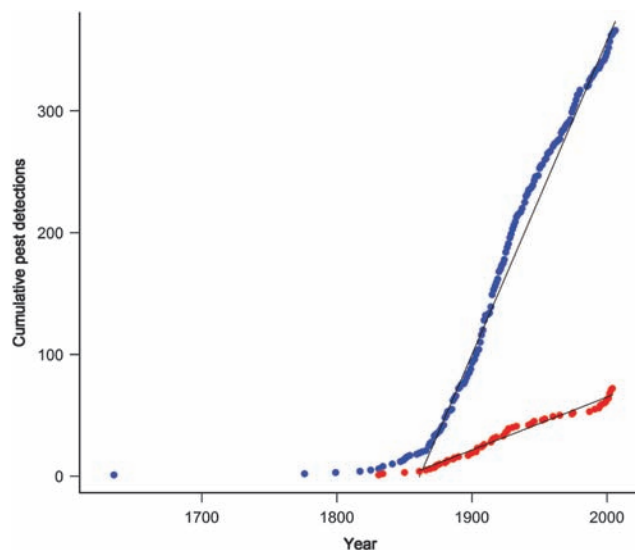

Figure 1. Cumulative detections of established forest pests over time with line fitted for the years 1860–2006. Nonindigenous insects (blue) were detected at a rate of approximately 2.5 insects per year (y = 2.58x − 4802; y = cumulative number of insects, x = year; r^2 = 0.988). High-impact insects and pathogens (red) were detected at a rate of at least 0.43 pests per year (y = 0.43x − 804.3; r^2 = 0.977).

be overdispersed Poisson distributed, and were regressed on guild (four classes) and interaction guild with a cubic polynomial of 10-year time units. The logarithm of time length was used as an offset covariate. Because of this offset in the model, the true response in the model is the count per 10-year interval (ratio). From the exploratory analysis, the model with the cubic polynomial best explained the data. We tested the differences in detection counts across guilds and time intervals. For the pair-wise comparisons we used Bonferroni-adjusted levels to achieve an experiment-wise error rate of 0.05 (figure 2b; table 1). We used SAS GLIMMIX and NLMIXED procedures (SAS 9.2, Cary, North Carolina) to estimate the parameters and test the pair-wise comparisons.

Table 1. Pair-wise comparisons of detection rates between feeding guilds of nonindigenous forest insects using fitted Poisson regression averaged over 18 time intervals.

Comparison rate	Estimated difference	Standard error	*p* value	Significance[a]
Foliage feeders, phloem and wood borers	2.63	0.83	0.0031	Yes
Foliage feeders, sap feeders	−2.00	1.00	0.2328	No
Foliage feeders, other	4.82	0.73	<.0001	Yes
Phloem and wood borers, sap feeders	−4.63	0.92	<.0001	Yes
Phloem and wood borers, other	2.18	0.61	0.0653	No
Sap feeders, other	6.81	0.83	<.0001	Yes

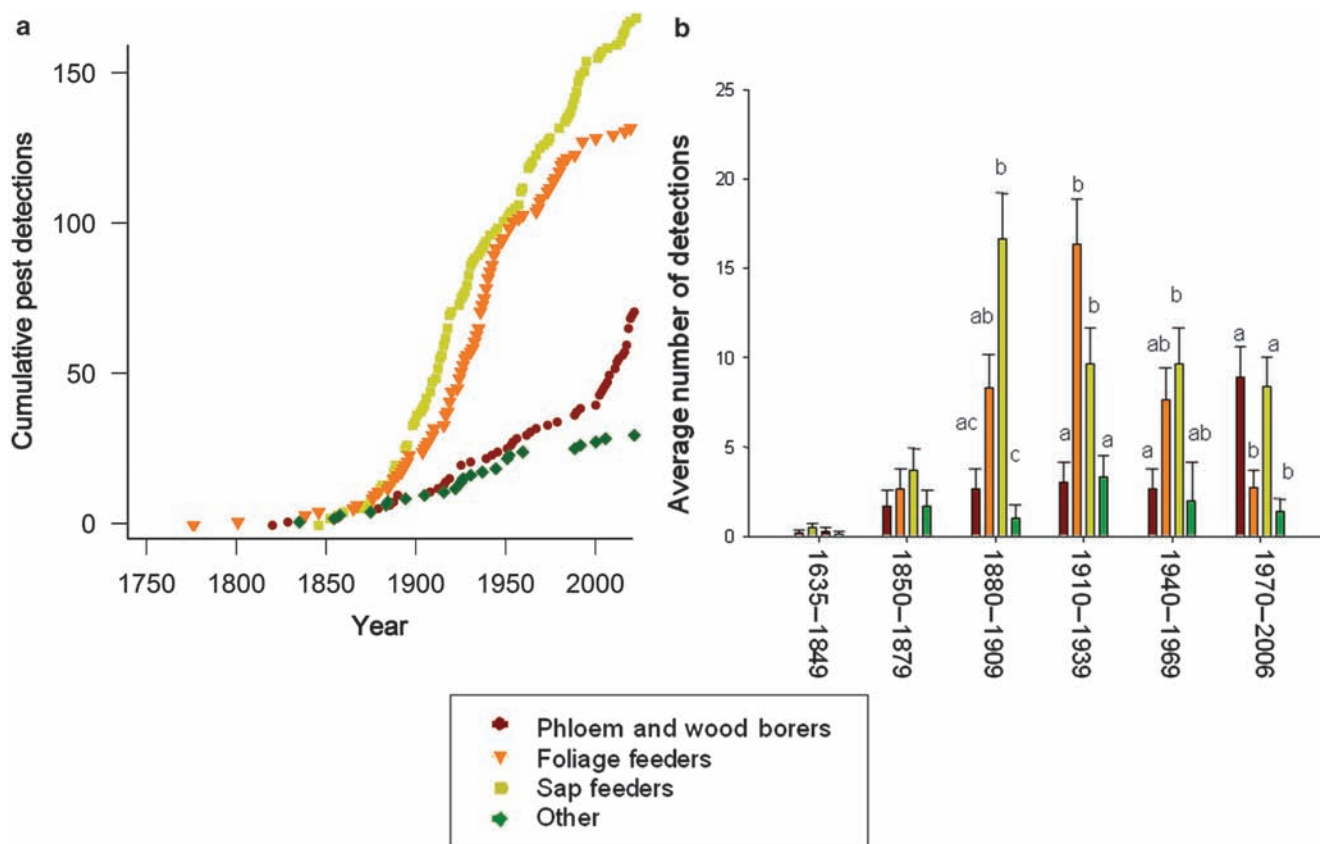a. Bonferroni adjusted α-level = 0.05/6 = 0.00833

Figure 2. (a) Cumulative detections of nonindigenous forest insects by guild over time and (b) the average count per 10-year period with approximate standard errors versus the six time intervals by guilds. Different letters indicate significant difference in detections between guilds at that time period based on pair-wise comparisons per period. Bonferroni adjusted $\alpha = 0.05/6 = 0.00833$ per guild.

Accumulation of nonindigenous forest insects

A total of 455 insect species representing 64 families and eight orders met our criteria for inclusion on the complete nonindigenous insects list. The first nonindigenous tree-feeding insect recorded in what is now the United States was the codling moth (*Cydia pomonella* [Linnaeus]), identified in 1635, and the most recent was the mimosa psyllid (*Acizzia jamatonica* [Kuwayama]), identified in 2006. Our list of species differed somewhat from similar compilations (Mattson et al. 1994, 2007, Langor et al. 2009) because we limited our list to species known to feed primarily on one or more tree species.

A key objective of our work was to assess the accumulation rate of nonindigenous forest insects in the continental United States over time. A total of 18 nonindigenous insect species were recorded from 1635 to 1859. From 1860 through 2006, however, the accumulation of nonindigenous forest insects was approximately linear ($r^2 = 0.988$; figure 1). Because we were missing dates of detection for 89 (20%) of these species, we calculated a minimum rate of 2.4 and a maximum rate of 3.0 species detected per year. We found no significant bias in the distribution of unknown dates among insect feeding guilds ($\chi^2 = 7.07$, degrees of freedom [DF] = 3, $p = 0.070$). Frequency of detection of nonindigenous forest insects began to increase in the late 1880s, and peaked from 1900 to 1930, when at least 111 known species were detected, representing 24% of the total list (figure 3). Since 1930, at least 167 new forest insect species (37% of the total) have been recorded. Between 1980 and 2006, at least 53 insect species, representing 12% of the total, were recorded (figure 3).

Representation of insects by taxa

Sap-feeding insects in the order Hemiptera dominated the list of nonindigenous forest insects with 189 species, accounting for 41.5% of all species (table 2). Aphids, adelgids, and scale insects in the suborder Sternorrhyncha accounted for 69% of the Hemiptera and 28.6% of all species on the complete list. Leafhoppers (Cicadellidae) were also well represented at 42 species, comprising 22% of the Hemiptera.

We included a diverse array of 119 beetle (Coleoptera) species, representing six families, on the list (table 2). More than half of the Coleoptera (53%) were assigned to the phloem- and wood-boring feeding guild. Ambrosia beetles and bark beetles (subfamily Scolytinae) represented approximately 34% and 10% of the Coleoptera, respectively. Only six buprestids were represented, all in the genus *Agrilus*. There were 38 beetle species classified as foliage feeders (32% of all Coleoptera), and 18 species were assigned to the "other" guild (e.g., root feeders).

Lepidoptera were represented by 87 species in 23 families (table 2). The microlepidopteran family Tortricidae accounted for 27 of the species (31%). Of the macrolepidoptera, the Geometridae were most diverse, with eight species on the complete list. Twelve Lepidopteran families were represented by a single species.

Other insect orders included eight families of Hymenoptera represented by 41 species. Sawflies and leaf miners in the Tenthredinidae (28 species) and Diprionidae (5 species) dominated this order. Four Hymenopteran families (Argidae, Cimbicidae, Cynipidae, and Eulophidae) were represented by a single species. There were also 13 species of Dipteran needle midges and leaf miners and four species of thrips (Thysanoptera). One termite (Isoptera: Rhinotermitidae) and one Orthopteran (Gryllotalpidae) were represented.

Feeding guilds and host breadth

The majority of nonindigenous forest insects introduced into the United States have been sap and foliage feeders (table 2). Four species of Thysanoptera were grouped with the sap feeders, although they could arguably be considered foliage feeders. Foliage feeders included Lepidoptera (76 species), Coleoptera (38 species), Hymenoptera (35 species), and Diptera (6 species). We classified 71 species as phloem or wood borers, which included 63 beetle species, along with five Lepidoptera, two Hymenoptera, and one termite (Isoptera). There were 37 species of seed, fruit, or root feeders, or gall makers assigned to the "other" guild, including a variety of Coleoptera (18 species) along with Diptera (7 species), Lepidoptera (6 species), Hymenoptera (4 species), one Hemipteran, and one Orthopteran.

Results of likelihood ratio tests from the fitted Poisson regression showed that detection rates differed significantly among the four insect feeding guilds (foliage feeders, sap feeders, phloem and wood borers, and other) ($F_{3,43} = 15.05$; $P < 0.001$), and the average number of detections varied significantly among year-class intervals ($F_{5,43} = 22.73$; $P < 0.001$). Differences in average rate of detection among feeding guilds varied depending on the time period studied as evidenced by the significant guild × year-class interaction ($F_{15,43} = 4.17$; $P = 0.001$). Across the entire time period studied, rates of detection were significantly higher for foliage feeders and sap feeders than for phloem and wood borers and species in the "other" guild (table 1, figure 3b). Rates of detection did not differ between foliage feeders and sap feeders or between members of the phloem and wood borers and the "other" guild.

The comparisons of guilds by time intervals are shown in figure 2b, confirming the differences visually observed in figure 2a. There were significant differences among individual guilds in the 1880–1909, 1910–1939, 1940–1969, and 1970–2006 time periods. Specifically, average detections of sap feeders were greater than detections of phloem and wood borers and detections of insects in the "other" guild in the 1880–1909 time period. In the same time period, average detections of foliage feeders were greater than for members of the "other" guild. From 1910–1939, significantly more foliage feeders and sap feeders were detected than phloem and wood borers, as well as members of the "other" guild. Average detections of sap feeders were significantly greater than the phloem and
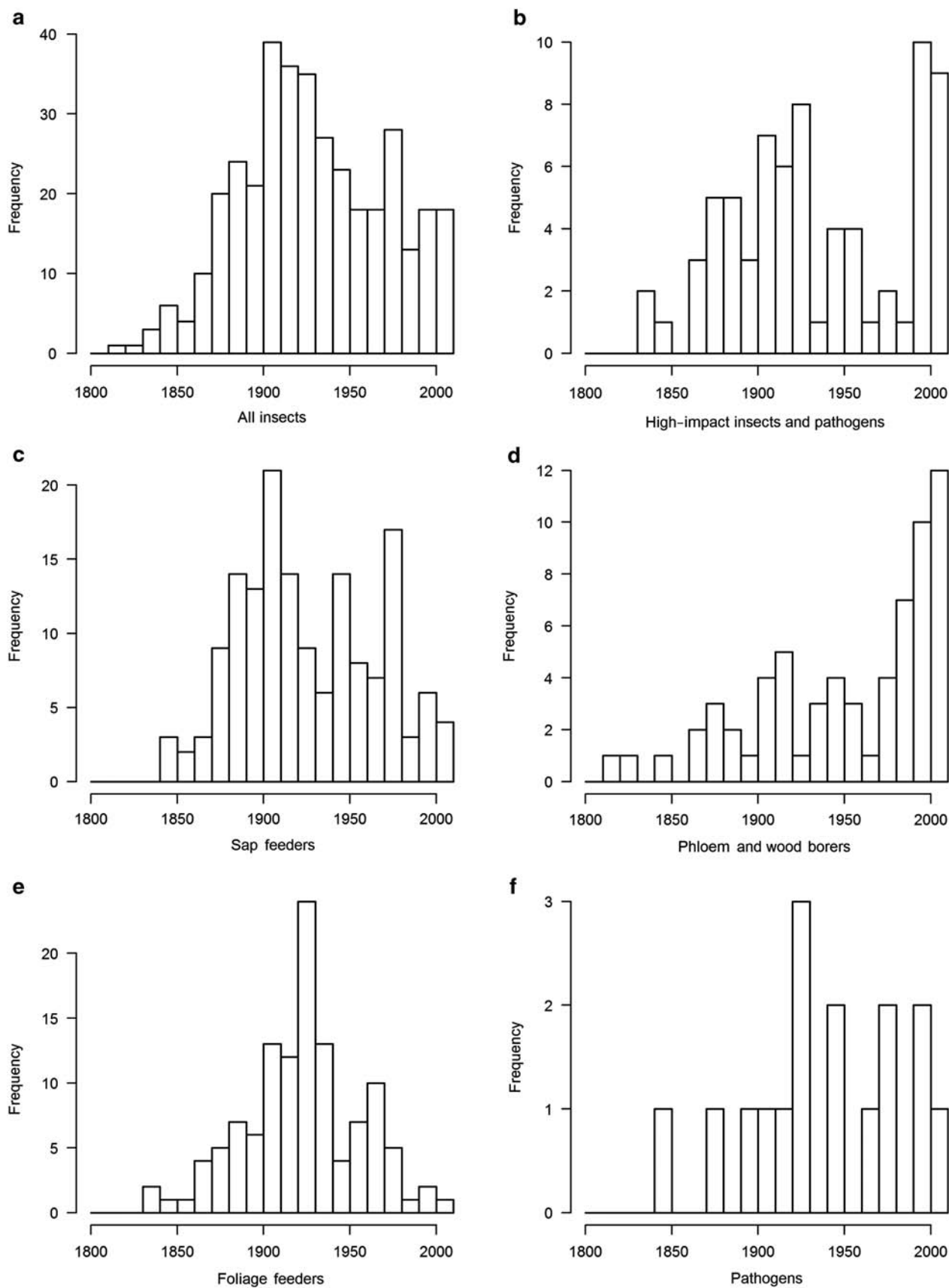
Figure 3. Frequency of detection over time of (a) all nonindigenous forest insects, (b) high-impact insects and pathogens, and (c–f) insect-feeding guilds.

wood borers in the 1940–1969 period. Last, there was a spike in the phloem and wood borers in the 1970–2006 time period; average detections of this guild and detections of sap feeders were significantly greater than detections of foliage feeders and members of the "other" guild.

Nearly half of the nonindigenous insect species (49%) were classified as monophagous because they feed on only a single host genus, whereas 33% were polyphagous, with a broad host range encompassing multiple families of hosts. The remainder were oligophagous species that feed on multiple genera of hosts within a single plant family.

High-impact insects and pathogens

Of the 455 insect species on the complete list, we assigned 62 insect species (14%) representing 25 families and six orders to the high-impact list, which included only insects of regulatory significance or species that have caused notable damage to forest or urban forest trees in the United States (see appendix). Only two insects on the high-impact list were detected before 1860: the black vine weevil (*Otiorhynchus sulcatus* [Fabricius]) (Coleoptera: Curculionidae) was detected in 1831, and the elm leaf beetle (*Xanthogaleruca luteola* [Müller]), a chrysomelid, was detected in 1834. The most recent record of a high-impact invader was for Mediterranean pine engraver (*Orthotomicus erosus* [Wollaston]), a bark beetle detected in 2004. We were missing the year of detection for six (10%) insect species on the high-impact list.

We also included 16 pathogens known to injure or kill forest trees in the United States on our high-impact list (table 3). Only one was detected before 1860: Phytophthora root rot (*Phytophthora cinnamomi* [Rands]) was detected in 1850. Nine of the 16 pathogens were Ascomycetes, including four in the Diaporthales and four in the Ophiostomatales. These included canker pathogens such as *Cryphonectria parasitica* (Murrill) Barr, which causes chestnut blight, and wilt fungi, such as *Ophiostoma* species, which cause Dutch elm disease. Two other Ascomycetes were canker fungi in the Helotiales. Three pathogens were Oomycetes in the Peronosporales; all were *Phytophthora* species, including the organism that causes sudden oak death. Three Basidiomycetes have been introduced, including two rust fungi in the Basidiomycota; the white pine blister rust pathogen, *Cronartium ribicola* J. C. Fisch, and the Eurasian poplar leaf rust pathogen, *Melampsora larici-populina*. The other Basidiomycete was *Amylostereum areolatum*, the pathogen associated with *Sirex noctilio*, a nonindigenous wood wasp.

From 1860 to 2006, damaging forest insect and pathogen species were detected at an average rate of between 0.47 and 0.51 species per year (figure 1), or one damaging insect or pathogen every 2.1 to 2.4 years. The frequency of detection of high-impact forest pests increased fairly steadily from the late 1880s until the early 1990s. More than half (56%) of the insects and pathogens on the high-impact list had been detected by 1930, if we exclude species with unknown detection dates. The frequency of damaging

forest pest detections then declined until approximately 1990. From 1990 to 2006, at least 19 nonindigenous species were detected, representing 24% of the organisms on the high-impact list (figure 3). Therefore, in this most recent 16-year period, detections of high-impact forest pests averaged 1.2 per year, nearly three times the rate of detections in the previous 130 years.

We found significant differences among insect orders (Fisher's exact, $p = 0.03$) and suborders (Fisher's exact, $p = 0.0027$) in the probability that a species would become damaging enough to qualify for the high-impact list. The orders Coleoptera and Hemiptera contributed the most insect species to the high-impact list (table 2), but there were fewer Hemiptera (particularly in the suborder Clypeorrhyncha) and more Coleoptera and Hymenoptera on the high-impact list than expected. Approximately 70% of the Coleoptera on the high-impact list were phloem or wood borers. All of the Hemiptera assigned to the high-impact list were in the Sternorrhyncha, which includes adelgids, aphids, scales, and psyllids. Of the four Thysanopteran species on the complete list, two species (pear thrips [*Taeniothrips inconsequens* Uzel] and basswood thrips [*Thrips calcaratus* Uzel]) were on the high-impact list. Hymenopterans were also relatively well represented on the high-impact list (table 2), with six sawflies, two leaf miners, and two wood borers. Only 10 of the 87 nonindigenous Lepidoptera species were represented on the high-impact list. Tortricids and geometrids, which had 27 and 8 species, respectively, on the complete list, were represented by only 3 and 1 species, respectively, on the high-impact list. In contrast, three of the four Lymantriids on the complete list were on the high-impact list. Of the 15 Lepidoptera families with three or fewer species on the complete list, only a single species, the mimosa webworm (F. Plutellidae) (*Homadaula anisocentra* Meyrick), was on the high-impact list. One Dipteran species, the European pine needle midge (*Contarinia baeri* Prell), and one termite (*Coptotermes formosanus* Shiraki), were on the high-impact list.

When we grouped insect species on the high-impact list by feeding guild, the foliage feeders, sap feeders, and phloem and wood borers comprised 42%, 32%, and 24% of the species, respectively. Only a single species from the "other" guild, the black vine weevil, was included on the high-impact list. Species in the phloem- and wood-borer and the foliage-feeding guilds were more likely to be on the high-impact list than expected, whereas fewer species than expected appeared in the sap-feeding and "other" feeding guilds ($\chi^2 = 9.75$, DF = 3, $p = 0.021$). Of the 192 species of sap-feeding insects, only 20 species (10.6%) were on the high-impact list. The high-impact list included 26 (16.8%) of the 155 foliage feeders and 16 (22.5%) species of the 71 phloem and wood borers.

Host breadth of the insect species on the high-impact list was similar to that of insects on the complete list. Of the high-impact species, 48% were classified as monophagous, 22% as oligophagous, and 29% as polyphagous. There was no relationship between host breadth and the likelihood that a species from the complete list would be included on the

Table 2. Number of nonindigenous forest insect species established in the continental United States as of 2006 by order or suborder and feeding guild.

Order	Number of families	Number of species	Percentage of total	Phloem and wood borers	Foliage feeders	Sap feeders	Other	Number of high-impact species	Percentage of high-impact species
Isoptera	1	1	0.2	1	0	0	0	0	0
Orthoptera	1	1	0.2	0	0	0	1	0	0
Thysanoptera	2	4	0.9	0	0	4	0	2	50.0
Diptera	4	13	2.9	0	6	0	7	1	7.7
Hymenoptera	8	41	9.0	2	35	0	4	11	26.8
Lepidoptera	23	87	19.1	5	76	0	6	10	11.5
Coleoptera	6	119	26.2	63	38	0	18	20	16.8
Hemiptera	19	189	41.5	0	0	188	1	18	9.5
Prosorrhyncha	2	14	3.1	0	0	14	1	0	0
Clypeorrhyncha	2	45	9.9	0	0	45	0	0	0
Sternorrhyncha	15	130	28.5	0	0	130	0	18	13.8
Total	**64**	**455**	**100**	**71**	**155**	**192**	**37**	**62**	**13.6**

Table 3. Nonindigenous forest pathogens established in the continental United States as of 2006 by order.

Order	Number of families	Number of species	Species
Diaporthales	3	4	*Cryphonectria parasitica* *Cryptodiaporthe populea* *Discula destructiva* *Sirococcus clavigignenti-juglandacearum*
Helotiales	2	2	*Lachnellula willkommii* *Gremmeniella abietina*
Ophiosto-matales	2	4	*Ceratocystis fagacearum* *Ophiostoma novo-ulmi* *Ophiostoma ulmi* *Raffaelea lauricola*
Peronosporales	1	3	*Phytophthora cinnamomi* *Phytophthora lateralis* *Phytophthora ramorum*
Uredinales	2	2	*Cronartium ribicola* *Melampsora larici-populina*
Venturiales	1	1	*Venturia saliciperda*
Total	**11**	**16**	

high-impact list ($\chi^2 = 1.1$, DF = 2, $p = 0.56$). Similarly, 44% of the pathogen species were monophagous, three species (19%) were oligophagous, and 37% were polyphagous.

Establishment rates for nonindigenous forest pests

The relatively constant rate of detection of nonindigenous forest insects and pathogens in the United States for the past 150 years was somewhat unexpected. Our analysis showed that overall, the rate of accumulation of nonindigenous forest insects in the United States has been approximately linear for the past 150 years. On average, roughly 2.5 new species of tree-feeding insects have been detected each year. Between 1860 and 2006, the time period encompassing the

majority of our data, international trade and travel escalated dramatically, presumably providing greater opportunities for the inadvertent introduction of nonindigenous insects or pathogens (Leimu and Koricheva 2004, Work et al. 2005, Liebhold et al. 2006, McCullough et al. 2006). Random samples of cargo arriving at US ports of entry and at the US–Mexico border suggest that despite quarantines and mitigation efforts, dozens of species of nonindigenous phytophagous insects continue to be introduced into the United States annually (Work et al. 2005). Using data recorded by inspectors from the US Department of Agriculture's (USDA) Animal and Plant Health Inspection Service, Work and colleagues (2005) estimated that more than 2000 species of plant-feeding insects most likely arrived in the United States between 1997 and 2001. Assuming even a minimal establishment rate of 2%, Work and colleagues predicted that 42 phytophagous insect species became established during that relatively short period of time. In addition, commodity transport historically required weeks, and nonindigenous insects had to survive long periods of transit. Modern transportation and refrigeration now enable species from around the world to arrive at ports of entry or borders in days or even hours, raising the probability that live insects will arrive on or within imported commodities or as hitchhikers.

In contrast to the linear rate of forest pest accumulation we observed over almost 15 decades, studies of historical patterns of invasion in aquatic, marine, and other terrestrial ecosystems have documented accelerating rates of accumulation for a wide variety of nonindigenous taxa (Cohen and Carlton 1998, Ruiz et al. 2000, Leppakoski and Olenin 2001, Ricciardi 2001, Wonham and Carlton 2005). These patterns are frequently cited as evidence of growing rates of introduction. Accelerating accumulation rates for other taxa have been variously attributed to higher propagule pressure (Ruiz et al. 2000) or "invasional meltdown" of recipient habitats (Simberloff and

Von Holle 1999, Ricciardi 2001). Enhanced efforts to detect and catalog invasive species could also introduce bias, generating accumulation rates that only appear to accelerate over time. However, examining null models shows that increasing rates of discovery can be generated even with constant sampling effort, introduction, and establishment rates (Costello and Solow 2003, Wonham and Pachepsky 2006). Our forest insect data were consistent with a null model that incorporates constant introduction and establishment rates, leading to an exponentially increasing cumulative number of nonindigenous forest pests (Wonham and Pachepsky 2006).

When we focused only on the high-impact pests, our analysis showed that a damaging forest insect or pathogen has been detected in the United States approximately every 2 to 2.5 years. This included 16 nonindigenous forest pathogens and almost four times as many insect species (62). Because of their microscopic size, there are virtually no estimates of how many fungi, bacteria, or other microorganisms have actually been introduced and become established but cause no discernible damage. Nonindigenous insects, in contrast, are more readily detected, and various survey efforts for nonindigenous insects have been undertaken by state and federal agencies. Overall, nearly 14% of the known established nonindigenous US forest insects have caused notable damage to forest or urban forest trees. This rate is similar to that of nonindigenous plants, where approximately 10% of the species that become established in a new habitat eventually become invasive (Williamson and Fitter 1996, Williamson 1999). If we consider only the insects detected between 1999 and 2006, however, 44% of the species introduced during this time period caused enough damage to warrant assignment to the high-impact list. This proportion could further increase if apparently innocuous insects behave as "sleeper species," a term used for species that eventually proliferate and cause damage 10 or more years after their establishment (NRC 2002).

Across all feeding guilds of insects, ecological and economic impacts of nonindigenous species clearly vary considerably. For example, the emerald ash borer (*Agrilus planipennis* Fairmaire) has killed tens of millions of ash (*Fraxinus* spp.) trees in the United States and is obviously a high-impact pest. In contrast, a nonindigenous congener, *Agrilus cyanescens* Ratzeburg, occasionally feeds in shoots of hardwood trees and shrubs, including invasive plants such as honeysuckle (*Lonicera periclymenum*), and to date has caused virtually no noticeable impact. Although insects from all guilds were assigned to the high-impact list, phloem and wood borers and foliage feeders were more likely than expected to cause some type of notable impact. Even within the high-impact list, the damage associated with species varies substantially, ranging from insects that cause minor defoliation or aesthetic injury to insects that cause extensive tree mortality.

Drivers of nonindigenous forest pest accumulation

The influence of increased trade and travel on the arrival of nonindigenous insects may be countered to some

extent by greater mitigation and regulatory efforts. As the devastating effects of some invasive species have become apparent, quarantines have been imposed to reduce the inherent risks of global trade and travel, and mitigation measures are now required, such as preshipping pesticide treatment, or pre- and postshipping inspections (NPB 1999). Although the overall accumulation of nonindigenous insects in the United States since 1860 has been linear, temporal peaks and declines are evident when records are compiled by decade. For example, detections of established nonindigenous insects in the United States peaked in the early 1900s then declined, presumably in response to gradual implementation of the 1912 Plant Quarantine Act (Sailer 1983). In Canada, nonindigenous plant pest detections peaked from 1940–1959 but did not decline noticeably until the 1980s (Langor et al. 2009). This pattern was attributed partially to efforts in the United States to reduce new introductions, which subsequently reduced spread of nonindigenous insects into Canada, along with implementation of the 1976 Canadian Plant Quarantine Act (Langor et al. 2009).

Another factor that may contribute to the relatively steady accumulation rate of nonindigenous forest pests in the United States involves the eventual depletion of strong invaders from other continents combined with expansions in trading partners. When a specific commodity from a given region is imported over time, the insects likely to be transported with that commodity have many opportunities to arrive and become established in a new region. Previous studies have suggested that insect species that are invasive on multiple continents may be especially adept at hitchhiking or colonizing new habitats because of their biological attributes (Sailer 1983, Niemela and Mattson 1996, Mattson et al. 2007). Over time, as specific commodities originating in specific regions are sampled repeatedly, the number of potentially strong invaders may be depleted. Species native to Europe currently dominate the nonindigenous forest insect fauna in North America (Niemela and Mattson 1996, Mattson et al. 2007). Expanding trade between the United States and other world regions (Krugman 1995, Sachs and Shatz 1994) effectively samples a broader range of insect communities, some of which presumably include strong colonizers that have greater opportunities to invade the United States with increasing trade. Notable increases in interception rates at ports of entry for plant-feeding insects native to China and Vietnam, for example, co-occurred with normalization of relations and increased trade between the United States and those countries (McCullough et al. 2006).

Increasing numbers of phloem- and wood-boring insects

The variability we observed among insect feeding guilds in rates of detections over time may be related in part to changes in shipping practices or regulatory priorities. For example, detections of foliage-feeding insects spiked in the 1930s and

1940s, which may reflect increased emphasis on inspections of imported plants resulting from the 1912 Plant Pest Act (OTA 1993, Sailer 1983). Sap-feeding insects, which are often tiny, cryptic, and difficult to find, exhibited relatively steady rates of detection, other than a brief spike in the 1980s.

In contrast, phloem and wood borers accounted for only 11% of the insects detected between 1800 and 1930 but represented 56% of the new insect detections between 1980 and 2006. This pattern may reflect substantial increases in the volume of containerized shipping since 1980 (Cullinane and Khanna 2000), which often entails the use of solid wood crating, dunnage, and pallets. In addition, awareness of phloem- and wood-boring insects by regulatory officials, forest health specialists, arborists, and related groups increased following highly publicized detections of the Asian longhorned beetle in New York City and Chicago in the 1990s (Haack et al. 1997). Regulations pertaining to solid wood packing material were strengthened (Haack 2001, 2006, APHIS 2004) and some exporters replaced solid wood packing materials with materials less suitable for insect transport, such as particleboard or plastics (Haack 2006). The Early Detection and Rapid Response program, designed to detect nonindigenous phloem and wood borers new to North America, was initiated in 2001 by the USDA Forest Service. Five previously unrecorded species of bark or ambrosia beetles were identified in the first five years of the program's operation (Rabaglia et al. 2008). Thus, increases in the use of solid wood packing materials, combined with targeted surveys and more awareness of phloem and wood borers, may explain why borers are the only guild demonstrating a substantial increase in rates of detections in recent decades.

Detections of pathogens remained steady over time, despite improved regulatory efforts. Characteristics of pathogens such as their microscopic size, cryptic signs and symptoms, and latent period render them especially difficult to detect at ports of entry. Modern advances in molecular diagnostics remain technically difficult and costly, and they generally require too much time to employ routinely in inspection stations. At least 5 of the 16 forest pathogens on our high-impact list are vectored by insects and associations between pathogens and insects can effectively increase impacts if one or both organisms are nonindigenous. For example, native *Neonectria* fungi have little effect on American beech trees until the nonindigenous beech scale (*Cryptococcus fagisuga* Lind.) invades the forest, initiating beech bark disease (Houston et al. 1979, Houston 2004, Castlebury et al. 2006).

Life-history traits and insect establishment

Intuitively, biological and behavioral traits seem likely to affect the ability of a species to become established or invasive in a new habitat. As in previous compilations of nonindigenous insects, species in the suborder Sternorrhyncha represented more than 65% of the sap feeders on our list. Scales, aphids, adelgids, and other insects in this group, which are usually small and often cryptic, are presumably difficult to find during inspections. In addition, many of these species

are able to reproduce by parthenogenesis. Other groups of insects, including several of the Scolytinae beetles and all of the sawfly species on our lists, are also at least facultatively parthenogenetic (Wheeler and Henry 1992, Niemela and Mattson 1996). Parthenogenesis eliminates the need for mate finding, enabling even individual colonists to become established in a new location (Niemela and Mattson 1996, Langor et al. 2009). Several parthenogenetic insects are associated with polyploidy and high mutation rates, which can provide genetic variability within small populations (Bullini and Nascetti 1990, Niemela and Mattson 1996, Langor et al. 2009).

Another feature shared by the Sternorrhyncha insects is that they are sessile or relatively immobile during much or all of their lives. Presumably, these insects are more likely to arrive on or in close association with imported plant material, and less likely to arrive as hitchhikers compared with mobile insects that are free living for a substantial portion of their life cycle. Insects that arrive on, within, or near their host plant have a considerable advantage because at least one suitable host is readily available, and there is a good chance of phenological synchrony between the colonist and its host. In contrast, insects that arrive as hitchhikers, or those that are transported in wood packing material, must not only survive transit but also locate a suitable host at an appropriate phenological stage.

Host breadth is a biological trait that appears likely to be associated with the ability of insects to successfully establish and become invasive in a new habitat. Mattson and colleagues (2006) noted that colonists must rapidly locate suitable hosts not only for food but also for shelter and to facilitate mate location and reproduction. Polyphagous insects, able to feed and develop on a wide range of host plant species, should presumably be favored over monophagous insects with relatively narrow host ranges. Nearly half of the insect and pathogen species on our complete list and on the high-impact list, however, were monophagous, whereas only 33% and 29% of the insects, respectively, were polyphagous or oligophagous. Niemela and Mattson (1996) reported a similar pattern for European plant-feeding insects in North America. To some degree, this pattern may simply reflect the general development of feeding specializations by phytophagous insects. When insect fauna in Britain were sampled, for example, only 25% of the species were polyphagous (Bernays and Graham 1988, Bernays and Chapman 1994). Niemela and Mattson (1996) suggested the dominance of monophagous insects also reflected the similarity of vegetation in North American and European forests, and proposed that establishment of specialized Asian insects could be limited by lower overall floristic similarity. This limitation may depend strongly on the regions of interest, however. Host range appears unlikely to limit the establishment of specialized forest insects from temperate mesophytic forests in China, where genera of native trees are highly similar to those in US forests (NRC 2002).

The need for regulations

Nonindigenous insects and pathogens continue to profoundly affect US forest and urban forest ecosystems and the people and industries that depend on them. Invasive species, in concert with other anthropogenic disturbances such as land clearing and changes in fire regimes, have dramatically altered the composition and structure of many forests in the United States (Holmes et al. 2009). Furthermore, they have inflicted high costs on society, including direct market losses (e.g., timber and nursery industries), the costs of control and eradication, and the loss of nonmarket benefits, including wildlife habitat and carbon sequestration. Over the next 10 years, the emerald ash borer alone is expected to cost municipalities nearly $10 billion for landscape tree treatment or removal (Kovacs et al. 2010), and this phloem-feeding pest potentially threatens native ash (*Fraxinus* spp.) species across North America (Poland and McCullough 2006, Holmes et al. 2009).

Our results demonstrate that nonindigenous forest insects and pathogens continue to become established in the United States despite current regulatory measures designed to prevent this. Recent increases in detections of established phloem- and wood-boring insects are a particular concern, especially given the relatively high proportion of these insects that have caused notable damage. All feeding guilds of insects, however, can potentially yield species capable of causing serious damage, and our ability to predict impacts of nonindigenous species before their establishment is limited. Broad-based efforts to prevent arrivals of nonindigenous organisms are generally considered to be more effective than attempting to respond to species that have already established, or worse, become invasive (NRC 2002, Lodge et al. 2006). Strengthened regulations to prevent introductions of nonindigenous species through solid wood packing materials, nursery stock, wooden handicrafts, and other pathways, along with enhanced efforts to rapidly detect newly established forest insects and pathogens, are critical to maintaining the health of North American forests and wildlands (NRC 2002, Lodge et al. 2006, Magarey et al. 2009).

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