

The Evolving Role of Forest Inventory and Analysis Data in Invasive Insect Research

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Enabled by humans' ever-expanding trade and travel networks, invasive alien species are crossing borders worldwide at alarming rates (Haack 2006; Haack and Rabaglia 2013; Hulme 2009; Kaluza et al. 2010; Koch et al. 2011; Liebhold et al. 2006; Lodge et al. 2006; Perrings et al. 2005; Pyšek and Richardson 2010; Tatem 2009; Westphal et al. 2008). An astonishing 50,000+ non-native species have been introduced into the U.S. either accidentally or purposefully, and approximately 4,500 of those introductions have been arthropods (Pimentel et al. 2005). Furthermore, new establishments of non-native species (arthropods and others) continue to accumulate rapidly, at an average of six per year in California and 15 per year in both Hawaii and Florida (Center for Invasive Species Research 2014). In the mid-1990s, it was estimated that some 360 introduced insect species had become established in U.S. forests (Liebhold et al. 1995; reviewed by Moser et al. 2009). According to one estimate, about 30% of those introduced species have since become major forest pests (Pimentel et al. 2005). In a more recent study, Aukema et al. (2010) generated a list of 455 non-indigenous forest pests that had become established in the U.S. as of 2006. A few examples of high-impact forest insect pests include the beech scale [*Cryptococcus fagisuga* Lindinger (Hemiptera: Eriococcidae)], which is associated with beech bark disease; the European gypsy moth [*Lymantria dispar* Linnaeus (Lepidoptera: Erebidae)], which feeds on hundreds of plant species, especially oak

and aspen; the hemlock woolly adelgid [*Adelges tsugae* Annand (Hemiptera: Adelgidae); HWA], which attacks all age classes of both eastern hemlock [*Tsuga canadensis* (L.)] and Carolina hemlock (*Tsuga caroliniana* Engelm.); and the balsam woolly adelgid [*Adelges piceae* (Ratz.) (Hemiptera: Adelgidae); BWA], which kills firs (*Abies* sp.), and in particular, has virtually eliminated mature firs in Great Smoky Mountains National Park. Introduced to North America between 1890 and 1954, these four insects are now widespread in the eastern U.S. Newer threats include the emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), which is believed to have arrived in the Detroit, Michigan, area during or even before the 1990s (Siegert et al. 2014), and the redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae), the vector of laurel wilt disease, which was first detected near Savannah, Georgia, in 2002 (Koch and Smith 2008). Like the previous examples, these two species are certain to dramatically alter the composition of landscapes where their hosts occur.

The U.S. Forest Service conducts the longest-running, most comprehensive survey of forested lands in the United States via the Forest Inventory and Analysis (FIA) program. The program collects data on status, trends, and resource conditions for all forest lands in a consistent fashion across the U.S. Researchers, regulatory officials, and policy makers who deal with forest pests have found these data invaluable for answering questions about

past invasions and predicting the effects of current and future invasions. The primary objective of this paper is to illustrate some of the many ways in which FIA data have been utilized for analysis and management of forest pest invasions.

Forest Inventory in the United States

Forest inventories have a long and colorful history in the U.S. From the first statewide inventory of forest resources in Massachusetts in 1830 to the 1998 Agriculture Research, Extension, and Education Reform Act (Farm Bill), which largely shaped the current FIA program, a wide variety of stakeholders have demanded reliable, up-to-date information on the status of U.S. forests. FIA continues to evolve as stakeholder needs change and technology advances. Among other things, the most recent Farm Bill (Agricultural Act of 2014) emphasizes the role of FIA in biomass and carbon reporting and calls for increased statistical precision at finer scales. A complete history of forest inventory efforts in the U.S. is beyond the scope of this paper, but the interested reader can find much of that information in LaBau et al. (2007). The beginnings of the modern FIA program can be traced to the McSweeney-McNary Act of 1928, which formally recognized a comprehensive Forest Service research program, to include forest inventory. This was amended and supplemented numerous times, and eventually replaced by the Forest and Rangeland Renewable Resources Research Act of 1978. The 1978 law, like the 1928 law, called for broad-scale resource inventory. A prior law, the Organic Administrative Act of 1897, dealt primarily with establishing the National Forests but also contained provisions for their inventory and monitoring.

Forest inventory efforts began in earnest in the 1930s. By the 1960s, the Forest Service had conducted regional survey projects on a state-by-state basis for all of the lower 48 states. Some states with an abundance of forested land had already been re-surveyed by this time. These initial surveys set the groundwork for reporting on timber resources, primarily area and volume of productive timberland. This information is still central to FIA, but by the late 1960s and 1970s, stakeholders began demanding more current information on an expanded suite of forest attributes. By the mid-1990s, expanded analyses and access to data were primary stakeholder concerns. Many of these concerns were addressed in the 1998 Farm Bill referenced above. Several important changes and enhancements were made to the FIA program in response to the bill. Two major changes of particular relevance to entomologists were the switch from periodic to annual inventories and the integration of FIA measurements and Forest Health Monitoring (FHM) measurements on a systematic national sampling design. The FHM program, established in 1990, was a national plot system designed to measure specific forest attributes identified as forest health indicators (e.g., crown characteristics, lichens, soil properties, and others), primarily to detect the effects of air pollution. Prior to the changes initiated because of

the Farm Bill, field crews worked on one or sometimes two states at a time until all plots were completed, with intervals between inventories ranging from six to 18 years (Gillespie 1999). Under the new or “enhanced” FIA program (implemented after 1999), a proportion of plots across each state are measured annually—including the FHM forest health indicators—and a report for each state is generated every five years, with ancillary publications and periodic updates as needed (Smith 2002).

While a detailed explanation of FIA sampling design, protocols, and estimators is not appropriate here, a basic understanding of FIA data requires a brief explanation and a few definitions. For a more comprehensive treatment of the FIA sampling frame, plot design, estimation methodology, and data analysis, the reader is referred to Bechtold and Patterson (2005). The FIA program is conducted in three phases. In Phase 1, land areas are stratified using remotely sensed data. The primary strata are “forest” and “non-forest,” although there is flexibility to use additional strata regionally. In Phase 2, field crews physically measure traditional FIA variables on individual trees within sampling plots: species, diameter at breast height (dbh), height, and status (alive or dead). They also assess quality of marketable timber, document invasive plant species, record condition classes present in the plot (changes in land use or vegetation that occur along more or less distinct boundaries), and determine forest type, among other things such as disturbance and treatment history. In Phase 3, additional observations and measurements, carried over from the FHM program, are made pertaining to forest ecosystem health.

A panel, or sub-cycle, refers to the plots measured within a state in one inventory year. This is generally 1/5th, 1/7th, or 1/10th of the total plots within the state. Thus, a full cycle of measurements for all plots in a state is completed every 5, 7, or 10 years (depending on area to be measured and funding). Each plot is comprised of four fixed-radius subplots (Fig. 1) and is randomly

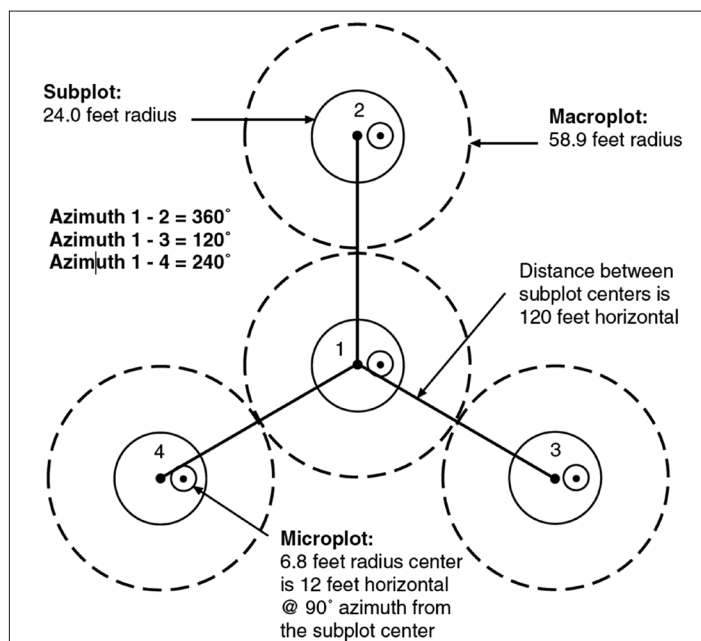


Figure 1. Schematic of a Forest Inventory and Analysis plot. From Bechtold and Patterson (2005).

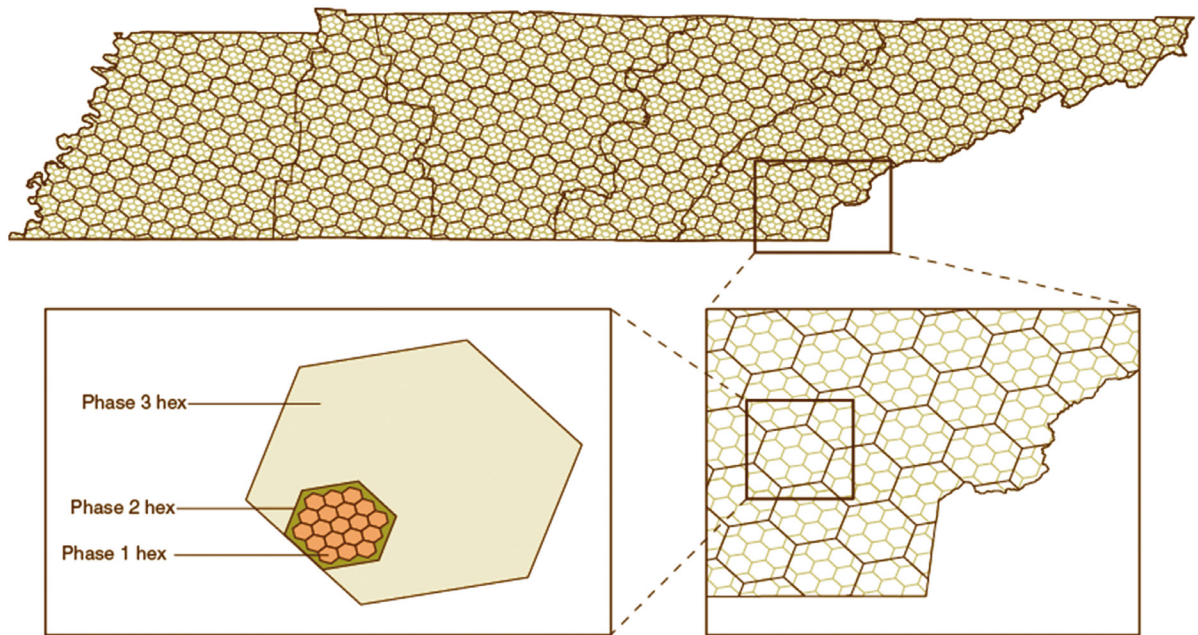


Figure 2. An example of the FIA hexagonal grid (Tennessee).

located within a hexagonal area of approximately 6,000 acres (2,428 ha). These adjoining hexagons are part of a base hexagon that covers the continental U.S. (Fig. 2) (White et al. 1992). Exact plot locations are kept confidential to protect the privacy of landowners and to preserve the integrity of the plots. Publicly available data are perturbed (relocated to a random location within approximately 1 mile of the actual plot) and swapped (up to 20% of locations are swapped with another, similar plot within the same county) (Lister et al. 2005). This maintains landowner confidentiality and protects the integrity of the plots, but does not affect coarse-scale estimates (McRoberts et al. 2005) or accuracy of spatial interpolation models (Coulston et al. 2006).

FIA data are available online from as early as 1968 (South Carolina), but dates of availability vary widely among the states. Many southern states have data online from the early 1970s to the present. In 2000, the state of Washington completed the new annual inventory, becoming the last state (with the exceptions of Hawaii and interior Alaska) to make annual estimates available through the FIA database. Earlier data can be found in various state reports, using the USDA Forest Service Research and Development “Treesearch” (<http://www.treesearch.fs.fed.us/>). It is worth noting that as the FIA program has evolved since its inception around 1930, methods and definitions have changed, and sometimes historic data may not meet current needs. Rudis (2003) discussed some of these changes in the context of varying perspectives, data sources, and purposes.

FIA data can be accessed through several free online tools (<http://www.fia.fs.fed.us/tools-data/default.asp>, last accessed 4/6/2015). Tutorials are also available, and it is wise for new users to familiarize themselves with the tools by working through the tutorials and documentation. Forest Inventory Data Online (FIDO) is perhaps

the most intuitive, but least powerful, tool for generating tables and maps using FIA data. FIA Data Mart contains comma-delimited data by state (<http://apps.fs.fed.us/fiadb-downloads/datamart.html>, last accessed 4/6/2015). EVALIDator allows users to generate customized tables or maps, either by state or using a circular area retrieval tool (<http://apps.fs.fed.us/Evalidator/evalidator.jsp>, last accessed 4/6/2014). More advanced users with knowledge of Structured Query Language (SQL) can specify polygon retrievals. FIA Spatial Data Services personnel are also available to help users in a variety of ways. They can help facilitate access to FIA data while protecting plot confidentiality. As part of that function, they can connect geographic information system (GIS) data layers and other geospatial data with FIA plots (i.e., with actual plot locations) on behalf of the user. They can also assist with summarizing data over an area of interest or otherwise provide information and expertise regarding the FIA database. Across the four administrative regions of FIA (Fig. 3), there were more than 800 significant user consultations in 2013, comprising more than 8,000 person-hours. The bulk of those consultations were with customers in academia, but other frequent customers included personnel from other government agencies, commercial entities, and policy makers.

As with any sampling program, FIA has inherent strengths and weaknesses that merit consideration. In general, the FIA sampling design is extremely robust and comprehensive, providing a statistically representative sample of forest conditions across the U.S. The plot observations made by FIA are thoroughly dispersed through space and time and are not conditioned on (or optimized for) any of the underlying sub-populations of interest. For these reasons, the FIA design is more readily adaptable to observations of other (previously unintended) populations than previous forest inventory designs have been. Another strength that resulted from the switch to an annual inventory is re-measurement of individual

trees over time, enabling researchers to track condition of individual trees and quantify tree-to-tree variation. One weakness of the FIA sampling design is the paucity of information on the urban forest resource. The 2014 Farm Bill (referenced above) calls for additional sampling in urban areas—welcome news to invasive species biologists, who recognize that new invaders often become established in centers of commerce such as port cities. So, while the lack of regular sampling in urban areas is currently a weakness of FIA, that situation is changing. A more detailed discussion of urban forest inventory is presented later in this paper.

Invasive Species Strategies and Research

With the implementation of Executive Order 13112 in 1999, which established the National Invasive Species Council, federal agencies were directed to take a number of steps aimed at prevention, detection, monitoring, restoration, research, and education as they relate to invasive species (Federal Register 1999). In 2004, the U.S. Forest Service published the National Strategy and Implementation Plan for Invasive Species Management (USDA Forest Service 2004). This was superseded by the Forest Service National Strategic Framework for Invasive Species Management (USDA Forest Service 2013), which incorporates the Invasive Species Systems Approach (ISSA). This approach specifies four key invasive species program elements: (1) prevention, (2) detection, (3) control and management, and (4) restoration and rehabilitation. Within each of these elements are a number of actions, many of which are directly supported by FIA data. Within prevention, for example, the ability to “identify vulnerable ecosystems” requires knowledge of host plant density. Within detection, the ability to “survey aggressively to detect new invasive species and monitor priority species” also depends on FIA data, which enable regulatory agencies and others to concentrate their efforts in areas where invasive forest pests are likely to occur. It is worth noting that FIA collects data on invasive plant species, which addresses another detection action: “report invasive species detection findings in standardized databases.” These data may have relevance to entomologists engaged in biological control efforts or other research requiring knowledge of invasive plant distributions. Within the third element, control and management, host distribution data are of tremendous value for actions involving prioritization of treatment areas, rapid response to new infestations, and monitoring success. Indeed, continuity of FIA data collection and reporting will be of increasing importance in the future as entomologists, foresters, and others monitor the status of

invasive species, their impacts, and the relative success of control measures. Finally, restoration and rehabilitation also require prioritization and monitoring, and FIA data can yield useful information about invasive species impacts, natural resources, fire susceptibility, and other relevant forest attributes. With intensification (multiplicative increases in sampling accomplished by subdividing the hexagonal sampling grid), errors associated with estimates decrease and FIA data are of greater utility for monitoring in areas of special interest (e.g., national forests and national parks).

Risk Assessment and Mapping

After Executive Order 13112 was implemented, the science of invasive species risk assessment gained new recognition in the U.S. Furthermore, certain international agreements, especially the most recent (1997) revision of the International Plant Protection Convention (IPPC), coupled with the establishment of some high-profile and destructive invasive species in the last two decades, have brought risk assessment activities to the forefront worldwide. (For additional information, see www.invasivespecies.gov). Besides the Forest Service, several other agencies, domestic and international, have interests and responsibilities in the risk assessment arena (Andersen et al. 2004a; Baker et al. 2005; Burgman et al. 2014; McKenney et al. 2003).

All risk assessments for potential invaders seek answers to a few common questions. First, what is the probability of arrival, establishment, and spread (Bartell and Nair 2003; Liebhold and Tobin 2008; MacLeod et al. 2002)? Second, what is the geographical extent of an organism’s future range (Jiménez-Valverde et al. 2012; Venette et al. 2010)? Finally, what are the likely ecological, economic, and sociological impacts (Andersen et al. 2004a, b; Morin et al. 2005; Yemshanov et al. 2009a, b)? Data readily available from the FIA program in the U.S., and strategic forest resource surveys in other nations (for

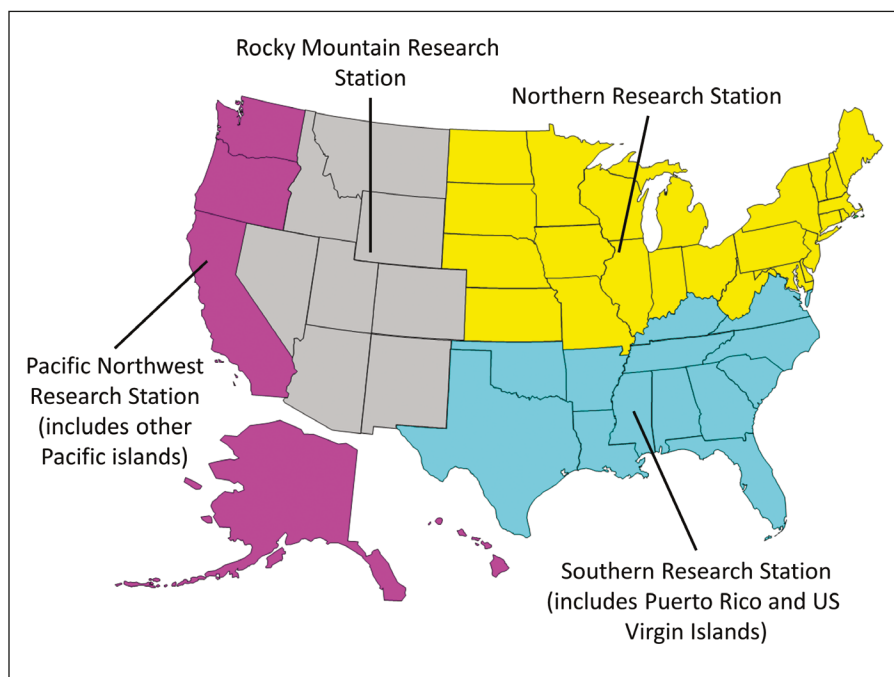


Figure 3. Forest Inventory and Analysis administrative units.

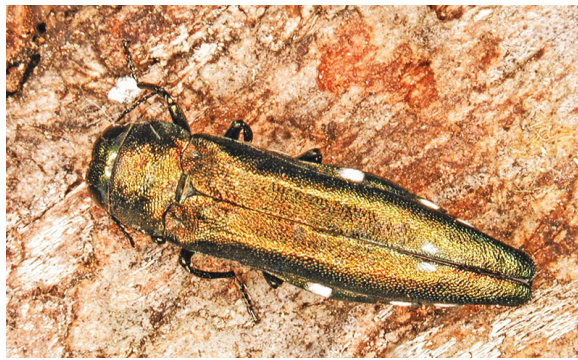


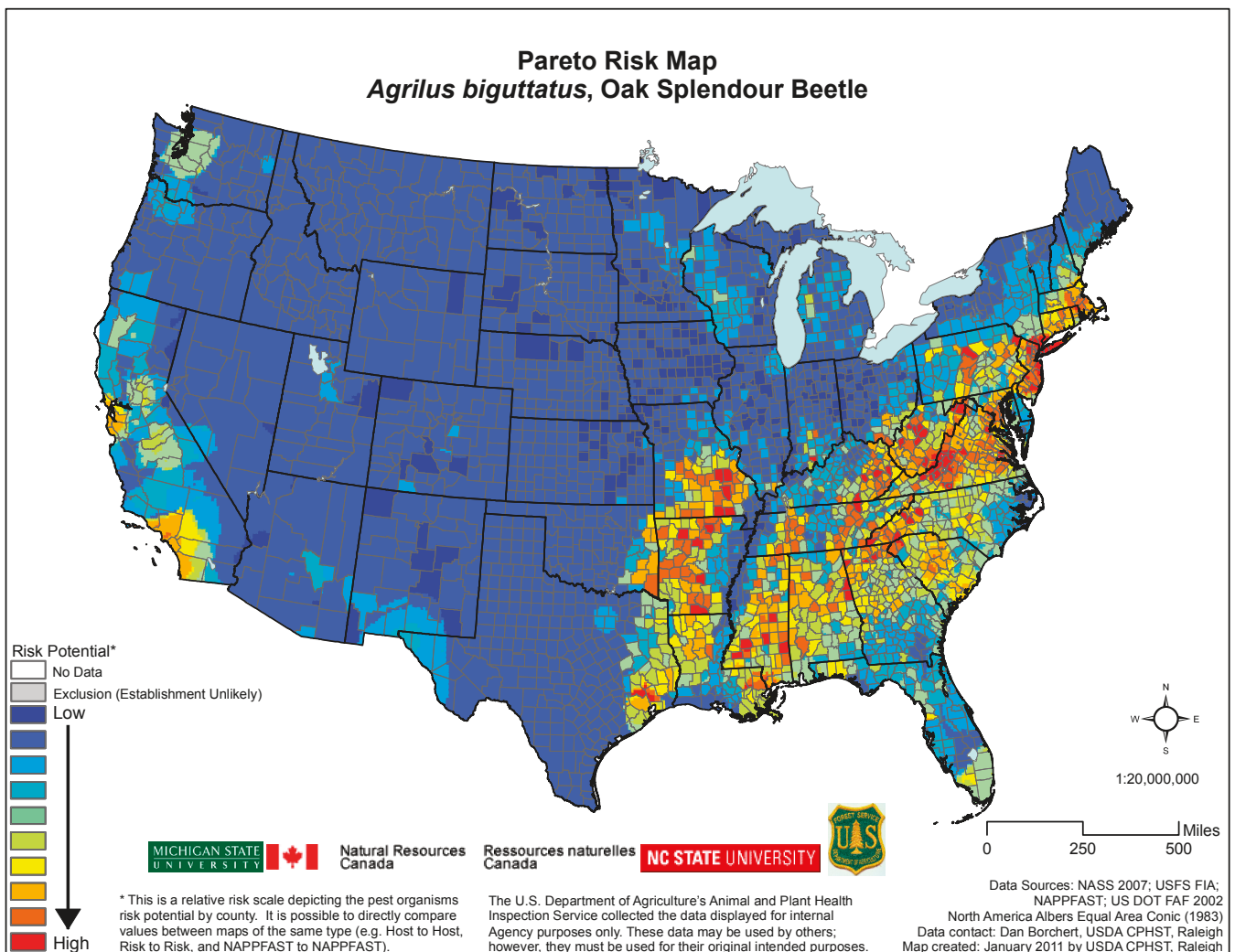
Figure 4. Oak splendor beetle, *Agrilus biguttatus* Fab. Photograph by Gyorgy Csoka, Hungary Forest Research Institute, Bugwood.org.

example, Canada's National Forest Inventory, <https://nfi.nfis.org/home.php?lang=en>; last accessed 4/6/2015) are directly applicable to all three questions, and in particular, are the primary source of information on current host distributions for broad-scale risk-mapping activities for invasive alien forest pests.

Risk maps, which are the geographic representations of underlying risk assessments, are powerful tools for conveying the potential for invasive species to expand their

range nationally and globally (Venette et al. 2010). One extensive collection of invasive species risk maps that utilizes FIA data to depict host distribution and abundance was constructed to support the Cooperative Agricultural Pest Survey (CAPS), a joint Federal and State program supporting surveillance for non-native plant pests (<http://www.nappfast.org>, last accessed 4/6/2015). These maps address risk for 50 species identified as significant threats to forest and agricultural resources in the U.S. For the forest pests on the CAPS Top 50 list, a team of researchers (see Magarey et al. 2011) utilized county-level host data from the FIA FIDO tool, along with climate matching techniques and the known world distribution of each pest, to map relative risk of growth and establishment across the U.S. Similarly, the U.S. Forest Service's Forest Health Technology Enterprise Team (FHTET) has developed a suite of national-scale risk map products that address both potential pest threats (i.e., species that have not been detected in the U.S., but are commonly intercepted at U.S. ports of entry) as well as pests, such as the siren woodwasp [*Sirex noctilio* Fabricius (Hymenoptera):

Figure 5. Pareto risk map for oak splendor beetle, *Agrilus biguttatus* F. (courtesy USDA Animal and Plant Health Inspection Service).



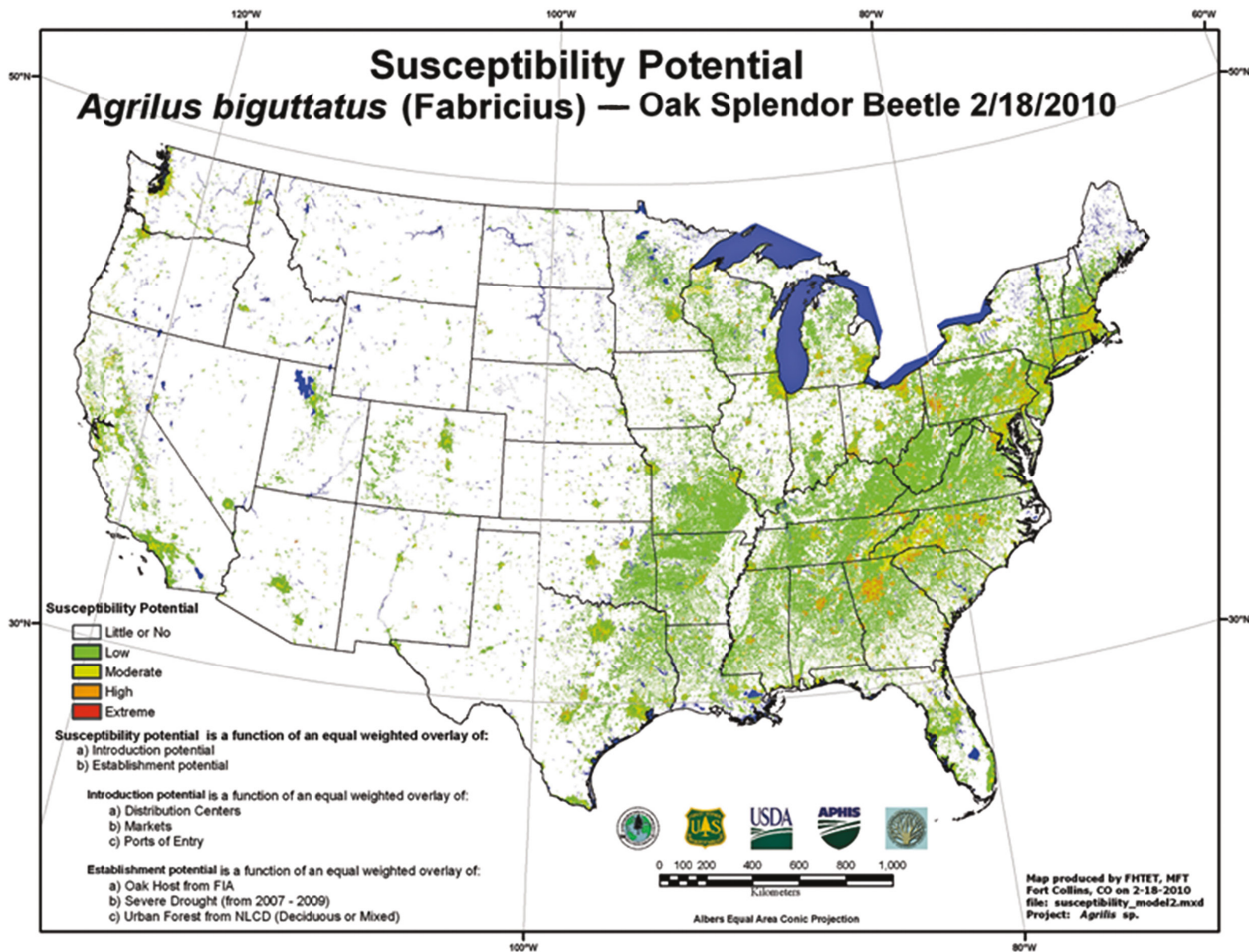


Figure 6. Susceptibility potential (equally weighted overlay of introduction potential and establishment potential) for oak splendor beetle, *Agrilus biguttatus*. Available online at http://www.fs.fed.us/foresthealth/technology/pdfs/agrilus_biguttatus_susceptibility.pdf (last accessed 06/03/2014).

Siricidae)], that were recently discovered in the U.S. and are anticipated to become widespread (see http://www.fs.fed.us/foresthealth/technology/invasive_species.shtml#InvasiveSpeciesRiskMaps, last accessed 4/6/2015). The approach typically employed by FHTET follows a multi-criteria framework in which different geospatial data sets (Marsden et al. 2005), or “criteria,” representing factors that affect the invasion process are weighted and combined based on expert opinion.

The oak splendor beetle [*Agrilus biguttatus*] (Coleoptera: Buprestidae) (Fig. 4) serves as a good example of risk model development using FIA data as the major determinant of host distribution. Although this European species has never been detected in the U.S., it is seen as a potential threat for several reasons: it is closely related to the emerald ash borer (EAB), is a relatively strong flier, and populations of this beetle have been linked to oak decline in its native range (Moraal and Hilszczanski 2000). Both FHTET and CAPS have produced risk maps for the oak splendor beetle. A “Pareto” risk map created for the CAPS program (Fig. 5) aggregates host abundance (based on county-level estimates from FIA), climatic suitability, and human-mediated pathways risk into a single product based on the Pareto dominance principle, which serves as the foundation of an objective, quantitative

method for combining multiple risk criteria (Magarey et al. 2011; Yemshanov et al. 2013). This map is targeted specifically toward decision makers, for whom a single product representing all major risk factors is a useful tool. The FHTET approach, on the other hand, results in three map products: introduction potential, establishment potential, and an equal-weighted overlay of both, termed susceptibility potential (Fig. 6). In particular, the establishment potential for the oak splendor beetle is largely based on a map of host abundance, developed through spatial interpolation of FIA plot data.

Generally, pest risk maps depict a species’ fundamental niche (the extent of the environments that are broadly suitable for its persistence) rather than the species’ realized niche, which is a subset of the fundamental niche defined by other important constraints such as predation, competition, and host availability (Venette et al. 2010). This is especially true for pest risk maps produced outside North America, which is a comparatively data-rich region. Despite their differing analytical approaches, the fact that both the CAPS and FHTET risk maps describe host distributions based on FIA data brings them closer to characterizing the realized niches of the target pest species. Arguably, this makes the maps more efficient and useful for decision-makers, who should have much

less at-risk area to consider when developing strategies to respond to these pests.

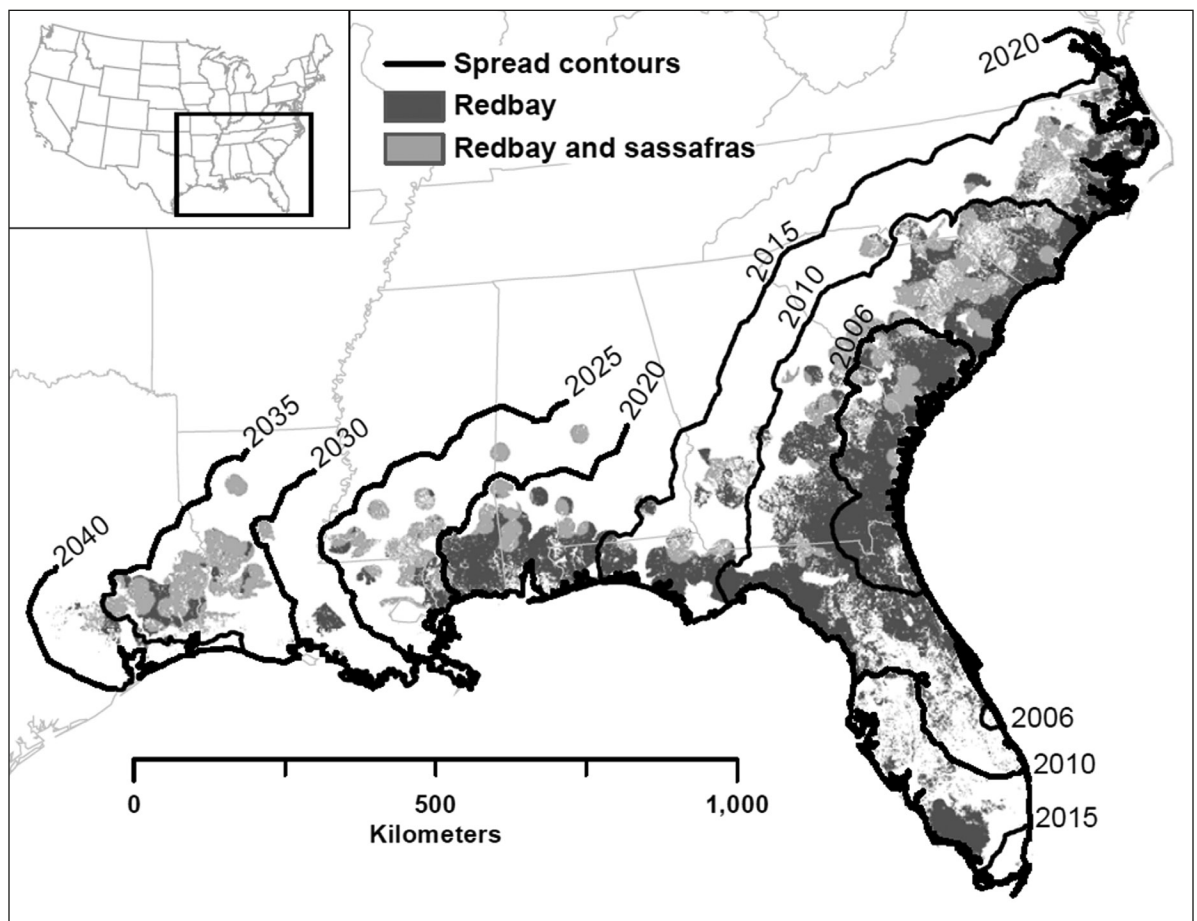
Quantifying Impacts of Invasive Pests

Forest inventory data are useful for predicting the ecological and economic impacts of invasive pests prior to their arrival as well as quantifying their impacts after introduction. For example, a look forward at potential spread and impact of the redbay ambrosia beetle and its fungal symbiont (*Raffaelea lauricola*), which is the causal agent of laurel wilt disease (LWD), paints a grim picture for southern coastal populations of redbay [*Persia borbonica* (L.)] and sassafras [*Sassafras albidum* (Nutt.)] (Koch and Smith 2008), the beetle's two primary host species in the U.S. Redbay lumber is used locally in areas where it is common, but the primary importance of this species (as is also true of sassafras) is to wildlife, with the fruits, leaves, and seeds all being consumed by various species (Goodrum 1977). The redbay ambrosia beetle has proven capable of attacking healthy trees (Mayfield and Thomas 2006), and upon inoculation, the laurel wilt fungus spreads quickly through a tree's vascular system, inducing

>75% tree mortality in many affected areas (Fraedrich et al. 2007). In their analysis, Koch and Smith (2008) used FIA data, along with climate and historical county-level infestation data, to predict the movement of the beetle; both the rate and pattern of spread were shaped by the amount of available host, as estimated from FIA measurements. All coastal populations of redbay are predicted to be infested by 2040 (Fig. 7). More recently, Shearman et al. (2015) fitted a quadratic model to FIA-estimated redbay populations range-wide from 2003 through 2011, demonstrating the slowing and potential reversal of redbay population growth. On a smaller scale, individual FIA plots had significantly fewer redbay stems/ha after arrival of LWD than before LWD, whereas plots that remained LWD-free had no differences between years.

Another example of a recently arrived invasive for which FIA data have played a key role in predicting impact and addressing some ecological questions is the emerald ash borer (EAB). Ash species are of tremendous economic importance. Black ash (*Fraxinus nigra* Marshall) is used for paneling, furniture, and basketry (Ward et al. 2009, and references therein). White ash (*F. americana* L.) is used for a variety of applications, including bows, baseball bats, tool handles, guitars, veneers, and joinery. Green ash (*F. pennsylvanica* Marshall) has been widely planted along urban streets in the U.S. In fact, the popularity of green ash as an urban forest tree in the wake of devastating losses of American elms [*Ulmus Americana* (L.)] from Dutch elm disease (*Ophiostoma* spp.) is thought to

Figure 7. Predicted extent of redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff, spread in the eastern U.S. through time, based on cost-weighted distance modeling from three points of origin, and overlaid on a map of host density. Cost-weighting was an inverse function of host density (redbay and sassafras); spread was faster in areas of high density. (Originally published in Koch and Smith 2008; reproduced with permission.)



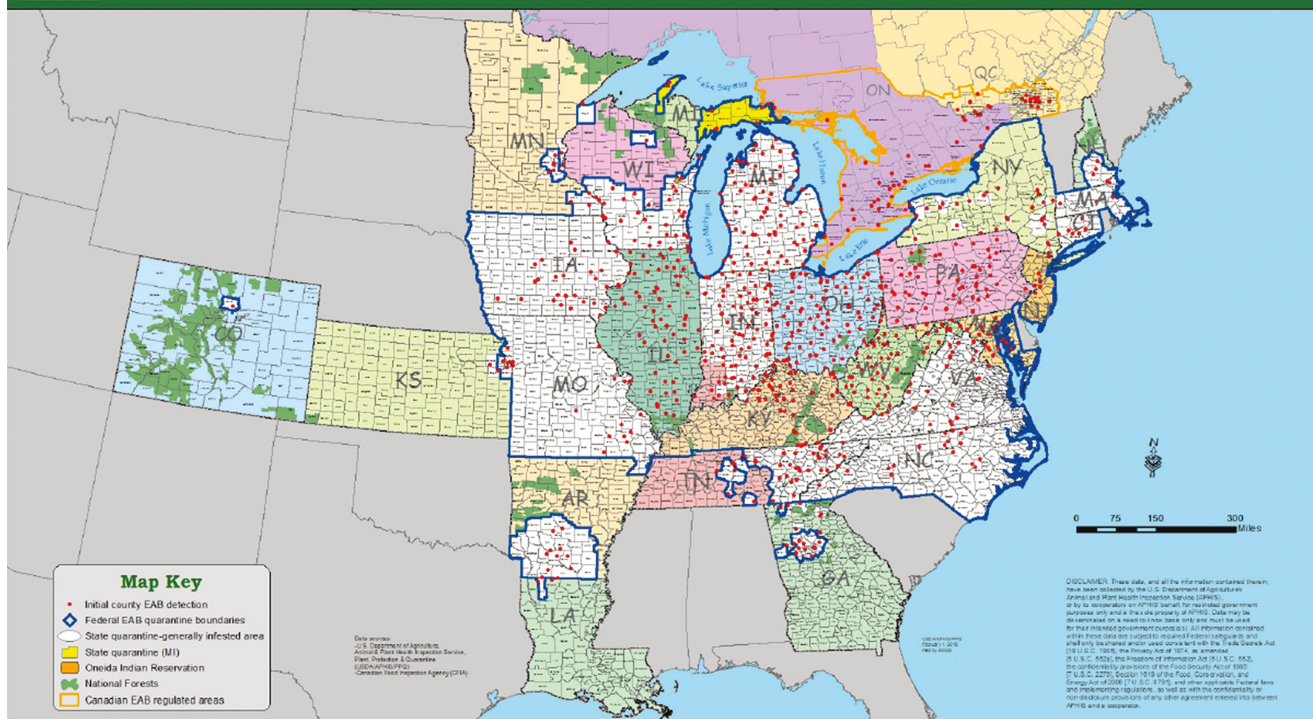


Figure 8. Emerald ash borer, *Agrilus planipennis*, distribution in the U.S. and Canada as of 1 May 2014. Available online at http://www.emeraldashborer.info/files/MultiState_EABpos.pdf (last accessed 06/03/2014).

have exacerbated the establishment and spread of EAB in the greater Detroit, Michigan, area (Marché 2012). EAB is capable of developing in and killing all North American ash species, although questions remain as to the order of preference among these hosts (Anulewicz et al. 2008). Larvae feed in the inner bark and outer cambium of host trees, disrupting nutrient flow and eventually girdling the tree. Death of infested trees can occur within 3–4 years of initial infestation (McCullough and Katovich 2004). Currently, EAB has been detected in 24 U.S. states and two Canadian provinces (Fig. 8). This incredibly rapid spread since the initial detection in Michigan’s Lower Peninsula roughly 12 years ago is thought to be due in part to movement of infested firewood (e.g., Haack et al. 2010), nursery stock, and logs.

One of the first challenges facing entomologists, modelers, GIS specialists, and others following EAB establishment in the U.S. was to assess the current state of the ash resource and develop reliable models to predict the movement and impact of the insect. Haack (2002) estimated that approximately 692 million ash trees (timberland only, not including urban trees) were at risk from EAB in Michigan. Poland and McCullough (2006) utilized FIA data to estimate that nearly 850 million ash trees in Michigan’s forests and riparian areas were threatened by EAB. MacFarlane and Meyer (2005) used FIA data to look at recent trends in the ash population in Michigan, concluding that ash populations in the area of the initial outbreak were not in general decline prior to the arrival of EAB. This finding was contrary to popular belief in light of long-time concerns about “ash decline” (Woodcock

et al. 1993; Ward 1997) and, as the authors point out, has implications for risk as it relates to the status of ash: widespread decimation of the ash population in the Great Lakes region since the early 2000s, initially thought to be the result of other biotic or abiotic factors, is almost certainly the result of EAB activity (Haack et al. 2002). DeSantis et al. (2013) utilized FIA data as the starting point for modeling the impact of EAB on forest composition over time in the Midwest and Northeast United States. As the authors pointed out, there is likely a disconnect between EAB effects in urban areas and effects across the broader landscape, due to the higher value of urban trees, preemptive harvest, and insecticide applications.

The European gypsy moth (*Lymantria dispar* L.) offers some other examples of how FIA data lend themselves to entomological inquiry—in this case, for an insect that has been in the U.S. for some time. May and Kauffman (1990) generated hazard ratings for potential gypsy moth defoliation across Tennessee using individual tree, stand, and site conditions from individual FIA plots, followed by an examination of dispersal potential as assessed using distance to the nearest road. They pointed out the difficulties in making inferences about small geographic areas based on the FIA sampling design. Gansner et al. (1993) used FIA data along with components of a previously developed defoliation potential model (Herrick and Gansner 1986) to generate a map of susceptibility potential across a seven-state region. They presented a discussion of the drawbacks of county estimates (primarily very high sampling errors) and examined shifts in susceptibility potential over time. A more broad-scale study was

completed by Liebhold et al. (1997), considering forest conditions across the U.S. as determined by FIA plots in the east, and FIA plots plus National Forest inventories in the west, where FIA did not inventory National Forest lands at the time of the study. They looked at historical defoliation in four northeastern states, and found the highest correlation between defoliation and proportion of land with >20 percent of stand basal area in species preferred by gypsy moth. Other variables that were highly correlated with defoliation included basal area of preferred species per acre, and proportion of land with >50 percent of stand basal area in preferred species. This was likely the first peer reviewed work to assess forest susceptibility to an invasive pest on a nationwide scale using FIA data.

Beech bark disease (BBD), caused by at least two species of *Neonectria* fungi in North America and facilitated by the feeding activity of the introduced beech scale, *Cryptococcus fagisuga* Lindinger, has been the subject of some interesting studies utilizing FIA data. As the exotic scale moves into new areas, its feeding activity alters the bark of beech trees, making it susceptible to entry by *Neonectria* fungi, which colonize the bark and kill it. Shigo (1972) described the progression of the disease as a series of three stages: the advance front (insects are found, but signs of fungal infection are scarce); the killing front (insects are obvious, and signs of disease widespread); and the aftermath stage (resistant trees remain, and microorganisms and insects may be attacking weakened trees). In the absence of other stressors such as drought and additional insect attacks, trees may live for many years; otherwise, mortality as high as 50% may be seen in as few as five years after infestation. Morin et al. (2007) used recent FIA data to examine potential relationships between beech basal area and rate of BBD spread, as well as relationships between standing dead beech and year of initial or predicted infestation with BBD. They also utilized historical FIA survey data to look for changes in forest composition resulting from BBD. No significant relationship was observed between beech density and the rate of beech scale spread, but there was a significant negative correlation between proportional beech mortality and timing of BBD. They observed a slight decrease in the relative abundance of beech as compared to associated species (sugar maple, *Acer saccharum* Marsh, and eastern hemlock, *Tsuga canadensis* L.), but an overall increase in volume in all but a few states as smaller beech stems made up for the volume lost to mortality of larger trees. Busby and Canham (2011) examined re-measured tree-level data in three states (Maine, Pennsylvania, and Michigan) representing a gradient of time since arrival of BBD (Maine being the earliest arrival, well over 50 years ago). They demonstrated current differences in size structure among the three states, demonstrating that left-skewedness of size distributions increased with disease severity: where BBD was present longest, there were more small trees and large trees were essentially eliminated. As one might expect, the data also revealed lower beech growth and survival in Maine. The authors went on to discuss overall loss of above-ground biomass due to BBD and the failure of sprouts and seedlings to

replace the biomass lost via death of mature trees. On a broader scale, encompassing the entire range of beech throughout the eastern U.S. deciduous forest, Garnas et al. (2011) clearly demonstrated size-specific mortality of larger beech and compensatory recruitment of small beech. To the authors' surprise, species that co-occur with beech did not exhibit compensatory recruitment in the wake of BBD. In a novel study examining the combined effects of two introduced pests on forest composition and succession, Morin and Liebhold (2015) used annualized FIA data to look at mortality and growth rates of beech and hemlock across a 22-state region where the distribution of BBD and HWA overlap. In an improvement over prior studies, they directly quantified mortality rates using re-measured plot data rather than using estimates of standing dead tree volume to quantify impacts (e.g., Morin et al 2007; Trotter et al. 2013). They found that annual beech mortality rates increase rapidly with increasing duration of BBD infestation up to about 15 years, then level off. Additionally, beech mortality rates were negatively associated with the interaction between BBD and HWA establishment duration. In other words, HWA establishment and subsequent hemlock mortality were beneficial to beech survival. Likewise, hemlock growth rates decreased with increasing duration of HWA invasion, and hemlock benefitted from beech mortality due to BBD. In the future, FIA data will shed light on the ultimate fate of forests where changes in stand dynamics due to BBD have not yet been fully realized.

While our intent in this paper is not to present an exhaustive list of works that have linked FIA or FIA-related data to entomological questions, some other studies bear mentioning. Morin et al. (2004, 2006) used FIA and FHM plot data in combination with aerial survey to address questions of defoliation frequency and its relationship with on-the-ground measurements of stand composition, tree health, and other variables. They developed maps of defoliation caused by a suite of three Lepidoptera, including gypsy moth, on the Allegheny Plateau in northwestern Pennsylvania using polygons from aerial survey, ultimately demonstrating that area-wide impacts of defoliation are generally less severe than impacts as measured in selected stands. In another study that contrasted stand-level impacts with regional impacts as demonstrated through broad-scale inventory, Trotter and others (2013) used FIA data from >400 eastern counties to characterize hemlock (*Tsuga* spp.) basal area (live and dead) over the course of about 20 years. They found that hemlock volume is generally still accumulating throughout the east, likely due to combined long-term effects of reforestation and succession surpassing the negative effects of HWA. In Massachusetts and Connecticut, however, where HWA has been present for an extended period, state-level data indicate that hemlock accumulation is either slowing or has stopped and hemlock may be in decline. Both of these studies effectively highlight the capability of FIA to capture broad-scale trends in forests, over wide gradients of temperature and other environmental conditions. Such broad-scale trends may differ markedly from more localized studies, such as Elliott and Vose (2011), who

noted rapid spread of HWA within an entire watershed in the southern Appalachians, resulting in >80% crown loss in four years following initial infestation, and Ford et al. (2012), who discovered >85% mortality of hemlock seven years after initial HWA infestation in western North Carolina.

Urban forest inventories are of tremendous interest to entomologists and others who work on invasive forest pests that are often introduced via transcontinental commerce into urban areas, where resource availability is critical to their establishment and initial spread. Urban forests also provide many unique functions to urban inhabitants, such as temperature modification, pollution mitigation, and aesthetic benefits. There may even be a direct link between trees and human health, as evidenced by a study that relied heavily on FIA data for deriving estimates of ash canopy cover (Donovan et al. 2013). Inventory data for Chicago's urban forest (Nowak 1994) were integral to estimates of ash density in BenDor et al.'s (2006) study on spatial dynamic modeling of EAB spread. Such work is important for assessing policies aimed at slowing the spread of EAB, and is valuable for estimating economic impacts. Sydnor et al. (2007) relied primarily on ash density estimates from a number of urban foresters and others with responsibility for urban forest resources in their work estimating potential impact of EAB in Ohio communities. Aukema et al. (2011) used FIA data along with additional data compiled from websites, publications, and city foresters to model economic impacts of multiple invasive forest pests in the continental U.S. Other authors (e.g., Kovacs et al. 2010) have utilized urban inventory data from multiple sources outside of FIA to estimate abundance of host trees (in their case, ash) in an effort to better understand the potential effects of EAB. They estimated the discounted cost of treatment, removal, and replacement of ash on developed land within communities at \$10.7 billion. The Forest Service has conducted pilot urban inventories in Indiana, Wisconsin, New Jersey, Tennessee, and Colorado through collaborative efforts between FHM and FIA (Cumming et al. 2008). A recent urban forest inventory has been completed for Tennessee (Nowak et al. 2012) and an inventory of urban forests across Texas is underway as part of a planned expansion of FIA activities in the urban arena. Other states for which urban inventories have been completed include Alaska, Washington, Oregon, California, and Hawaii. More work is needed, however, to increase coverage and integrate urban inventory into ongoing inventory efforts. For more information on national efforts to assess urban forest resources, see the USDA Forest Service's website on urban natural resources stewardship: <http://www.nrs.fs.fed.us/urban/> (last accessed 4/6/2015).

Scientists are finding other, novel ways to apply FIA data to questions about invasive species. Crocker and Meneguzzo (2009) examined relationships between EAB presence, host density, and landscape metrics derived from FIA data (forest proportion, edge length, and edge density). They found EAB presence to be associated with a low forest proportion, high percentage of ash, and high

relative edge density (essentially, highly fragmented areas of ash), demonstrating the utility of landscape variables collected by FIA in addressing questions about invasive pests. This is an area that merits further investigation and application. FIA data also support testing of broad hypotheses regarding invasions of forest pests. For example, Liebhold et al. (2013) examined geographical variation in invasive forest insects and pathogens, and observed that the majority of invasives are concentrated in the northeastern U.S. They attributed this spatial variation to propagule pressure and habitat invasibility. Increasingly, FIA data are also being used to address a number of questions around biogeochemical cycling. Some recent efforts have centered on carbon flux as it relates to large-scale disturbances from insects. For instance, Flower et al. (2013) described the potential effects of EAB disturbance on carbon mass and primary production in the midwestern U.S. In another study, Renninger et al. (2014) examined the effects of gypsy moth activity on mass of snags and coarse woody debris and subsequent changes in ecosystem respiration, using "FIA-like" plots in the Forest Service's Silas Little Experimental Forest in southern New Jersey.

In addition to predicting impacts, FIA data gathered under the newer annual inventory protocols are increasingly useful for assessing regional-level impacts during the course of invasions. Pugh et al. (2011) used 2009 FIA data to establish baseline ash distribution in the region surrounding the epicenter of the EAB invasion (Michigan, Wisconsin, Illinois, and Indiana). They then analyzed ash mortality, harvest, net growth, and several temporal trends in concentric zones of 50 km width radiating out from the epicenter. They were able to demonstrate elevated mortality (above baseline) and decreased net growth at varying distance from the invasion epicenter, as well as increased ratio of recently dead to live trees. Beyond 200 km from the invasion epicenter, the cause of death was indeterminate for most (77%) of the dead trees. Within 200 km, ash death was attributed to insects for 8% (150–200 km), 15% (100–150 km), 69% (50–100 km), and 80% (0–50 km) of dead trees. Volume, number of trees, and net growth decreased from the 2004 inventory to the 2009 inventory. Another ongoing research project has used multiple inventory cycles of FIA data to estimate the amount of redbay mortality across the southeastern U.S. since the arrival of the redbay ambrosia beetle. Preliminary estimates (Koch, unpublished data) suggest that nearly half a billion redbay trees, roughly 35% of all redbay in the Southeast, had died as of 2014, with Georgia (50% mortality) and South Carolina (46% mortality) impacted especially severely. As researchers look for ways to increase the utility of annualized inventory data for finer-scale estimates, it would not be surprising to see the data utilized in additional studies of this nature.

Forests are dynamic. In some areas, forests are aging, with potential impacts on host distributions as forest types change (as a result of succession) and, in some cases, increased susceptibility of older trees to various pests. Climate change is anticipated to have impacts on host distributions as well as survival and reproduction

of pests. As pests decimate populations of some tree species (e.g., *Fraxinus* spp. due to emerald ash borer) other species will increase in abundance. While rates of change vary greatly for different types of disturbance, it is evident that continued forest inventory will be needed to characterize our forest resources. Pests that invade U.S. forests are particularly vexing in light of heavy reductions over the past few decades in the number of pathologists, entomologists, and invasive plant scientists employed by federal agencies and universities, a trend pointed out by Moser et al. (2009) along with a call for increased inventory and monitoring efforts. Our intent in this paper was to provide a very limited sampling of research, regulatory, and policy-making efforts that are supported by FIA; there are many additional studies in the literature that have relied on FIA data in some way. The FIA program will continue to explore novel ways to help stakeholders answer questions about invasive insects and other biotic and abiotic forces affecting U.S. forests, just as users will continue to develop creative ways to maximize the utility of FIA data.

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