

## Article

# Generalist Pests Cause High Tree Infestation, but Specialist Pests Cause High Mortality

Qinfeng Guo \*  and Kevin M. Potter 

USDA FS—Eastern Forest Environmental Threat Assessment Center, 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA; kevin.potter@usda.gov

\* Correspondence: qinfeng.guo@usda.gov

**Abstract:** Whether specialist pests can cause more damage to their host plants than generalist pests is a critical issue in both basic biology and nonnative species management. To date, there is no consensus on how we define “specialist vs. generalist” pests and how we should assess forest damage or impacts (volume loss vs. mortality). Here, we comparatively investigate whether nonnative generalist pests may cause more damage to US forests than nonnative specialist pests using two frameworks: (1) the “binary or dichotomous approach” through a largely arbitrary classification of specialist and generalist pests, and (2) the “specialist-generalist continuum”. We measure damage or impact in two ways, one by the total host volume infested and the other by total host mortality. In the binary comparison, generalists infested more host tree volume per pest species than specialists, but the latter (mostly pathogens) caused higher mortality of host trees. The “specialist-generalist continuum” concept could reveal a different pattern regarding pest invasions and impacts when there is no clear separation between generalists and specialists in a community or region. Therefore, we suggest using the “continuum” approach to address related questions in future studies, thus offering new insights into pest invasions that have deeper implications for forest pest monitoring and management.

**Keywords:** binary or dichotomous comparison; disease; host richness; impacts; exotic pest invasion; specialist–generalist continuum



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## 1. Introduction

Both native and nonnative (or exotic) invasive pests (insects and diseases) can cause significant damage to native forest ecosystems and to the economy [1–5], but predicting which pests may cause more damage than others remains a major task facing ecologists. For simplicity and for broader monitoring and management applications, can pest species also be classified into different groups to aid in developing model predictions? There are indeed a variety of ways to classify species into different groups. For example, based on the evolutionary breadth of tree species they infest, invasive pests can be classified as specialists or generalists [6]. The former group has one or a very few, very similar, and generally closely related hosts and the latter has more hosts which are generally less closely related. However, there is no consensus on how to define a specialist or a generalist pest when different people prefer different ways of quantifying the damage caused by these pests. For example, the total host volume infested and host plant mortality are two common types of damage, but the ecological and economic implications of these types of damage may differ. When clear definitions of damage are given, answers regarding damage caused by specialists vs. damage caused by generalists to their host plants can be better quantified and

compared. The results based on such quantifications would be key to both understanding basic biology and informing invasive species management [7].

In both natural and social sciences, attempts to compare the performance and damage (or impacts) between specialist vs. generalist pests have generated several important concepts such as the specialist–generalist continuum (vs. binary or dichotomy), the specialist–generalist spectrum, and the specialist–generalist paradigm [8]. Most related studies to date have chosen a few species (or pairs of species)—not large or representative groups—for comparison, mostly due to financial, labor, and time constraints.

Along the first line of studies related to the possible effects of pest infestations, ecologists have grouped the plant community into hosts and nonhosts [9–11]. Particular attention has been given to host species, simply because they typically lose volume or suffer high mortality due to pest infestation, although the role of nonhost species is also gaining attraction, mostly because they also affect the performance of host species, e.g., through competition [11,12]. Along the second line of studies, researchers have classified pest species according to their diets, food consumption, and other factors [11,13,14]. For example, based on their feeding preferences, pests in a plant community can be grouped as specialists and generalists. The classification of host community species and pest species into different groups is useful as it can provide insights into invasion mechanisms and can aid in the development of monitoring and control priorities.

Previous studies on pest ecology and management have focused on the role of host vs. nonhost species in nonnative pest invasions and control mechanisms [2,11–13,15,16]. On the other hand, increasing effort is being made to examine the effects or impacts of invasive species, such as pests, on native tree species in forest ecosystems [2,7,17]. However, most of these studies have not specifically investigated the relative performance and impacts of specialist vs. generalist pests. Yet, in both theory and practice, a broader comparison between generalists and specialists is critically needed to better assess and quantify pest damage to forest ecosystems. For example, ecologists and managers need to know whether generalists could cause more damage to their hosts than specialists and whether different measures of damage could lead to different conclusions about pest impacts. For managers with limited resources, a key question is whether we should prioritize targeting generalists or specialists for monitoring and control based on the specific measure of damage they cause.

Most previous studies that have assessed forest pest effects have used host tree volume or biomass data, that is, how much of the host tree volume has been infested. However, due to data limitations, the overall effects of forest pests on host tree mortality have rarely been evaluated, although case studies on an individual pest vs. its host mortality already exist. Here, we comparatively assess the damage (loss of host tree volume or biomass vs. annual mortality rate of the host tree species) caused by nonnative invasive pests to United States forests between specialist and generalist pests. This is conducted comparatively using the dichotomous and continuum specialist–generalist approaches. We then discuss the possible mechanisms behind the observed patterns and the implications of our findings for monitoring and management.

## 2. Materials and Methods

We selected 66 species of nonnative forest insect herbivores ( $n = 51$ ) and forest pathogens ( $n = 15$ ) known to cause significant damage across United States forests for this study. These species are limited to herbivorous species that feed on foliage, sap, phloem, or wood and exclude predators, pollinators, and detritivores. We excluded parasitic plant species and pests that primarily infest horticultural trees and crops. We determined the number of host tree species for each of these insect and disease species, and we assessed

damage differences (as measured by the tree volume infested and tree mortality) among generalist and specialist pests. The tree volume data and mortality data (estimates) were derived from data collected by the US Forest Service's Forest Inventory and Analysis Program (FIA) [18], which are publicly available. More information about the FIA can be found at <https://research.fs.usda.gov/programs/fia> (accessed on 12 December 2024).

The information on host specialization and host ranges of pest species was derived from Liebhold et al. [13], which included a list of the primary tree species used as hosts by each pest compiled from the scientific literature, regulatory reports, university extension bulletins, and other related materials. Among the 66 pest species (Table S1), 15 were found to cause significant tree death and had been examined by numerous studies that focused on individual pest species, e.g., [2,19,20]. These species included 9 specialists and 6 generalists based on the same classification criteria used for the 66 pest species. Among the 9 specialists, 6 were pathogens, and among the 6 generalists, 3 were insects. Our preliminary analysis showed that pathogens and insects performed similarly in host infestation; therefore, we combined them in our generalist vs. specialist classification.

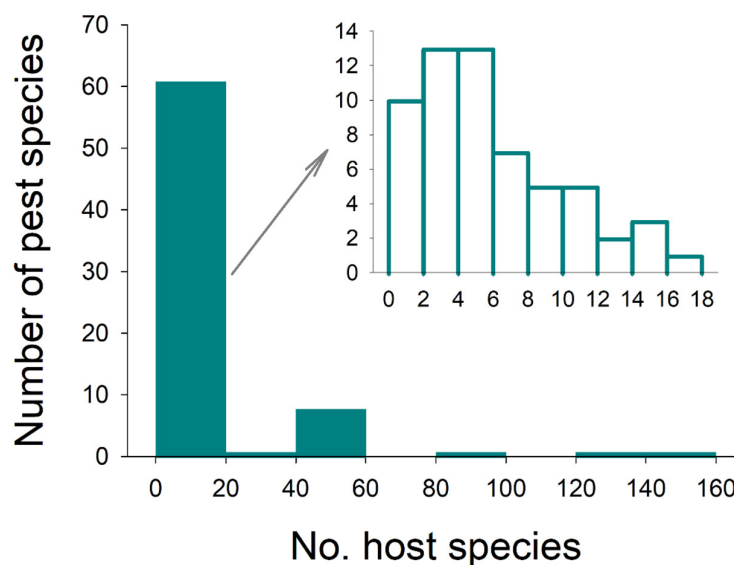
The tree volume of each species was estimated up to the county level using the FIA MapMaker online data query program [21] based on data from FIA inventory plots, and the volumes of each host tree species infested were then calculated and summed for each pest species, also up to the county level. The average annual mortality for the host tree species of these pests was estimated by comparing the number of live vs. dead trees between successive sampling years. For more details about the tree volume infestation estimates and mortality, see [2,13].

Since there is no universally accepted criterion to classify species as specialists or generalists, we adopted the definition by Ali and Agrawal [6], who defined “specialists” as those who consume a few related species and “generalists” as those who consume species in several plant families. Specifically, for the dichotomous approach, we classified the 66 pests with host species  $\leq 5$  as specialists and those with  $>5$  host species as generalists. This classification served two purposes: (1) balancing the number of species in each category for comparison, i.e., roughly half ( $n = 32$ ) of the 66 species examined were specialists and half ( $n = 34$ ) were generalists; and (2) ensuring the number of species in each category had a large sample size for statistical analyses.

Although a dichotomous classification in terms of host selection has, for the most part, been used for demonstrations, in reality, there may be a specialist–generalist continuum (or spectrum or gradient) in terms of the number of host species affected by pests, e.g., [22]. For this reason and for comparative purposes, to examine the possible effect of how a species was defined in terms of specialty in a broader context, we regressed host tree “damage” against the number of host tree species as an independent discrete variable. To examine whether host richness could facilitate the infestation rate, we also comparatively examined the role of time (years since first detection in the United States) in the tree volume infestation by specialist and generalist pests.

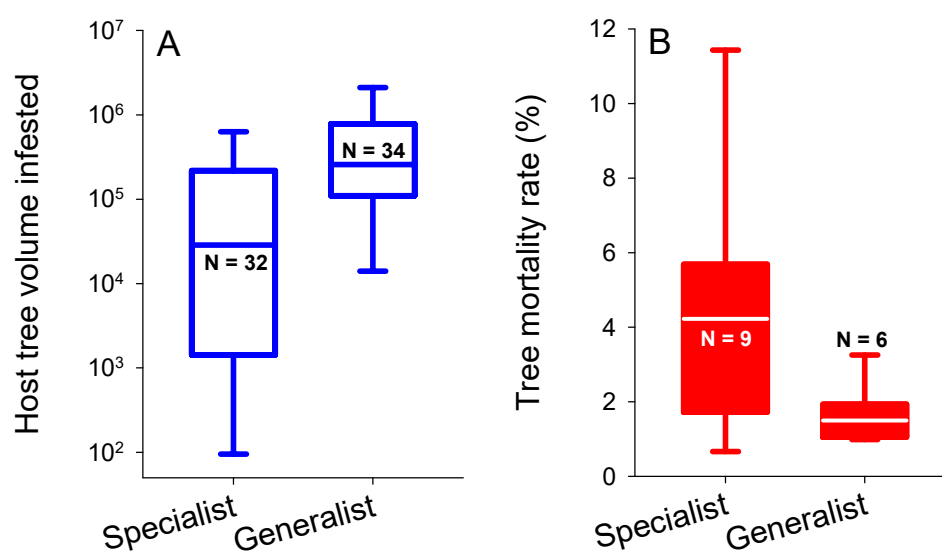
### 3. Results

We observed a clear specialist–generalist continuum of host tree species (not a clear dichotomy) among nonnative, invasive forest pests across the United States forest ecosystems. Most of the 66 nonnative invasive pest species had a few host tree species, and those with very large numbers of host species were very rare (Figure 1).



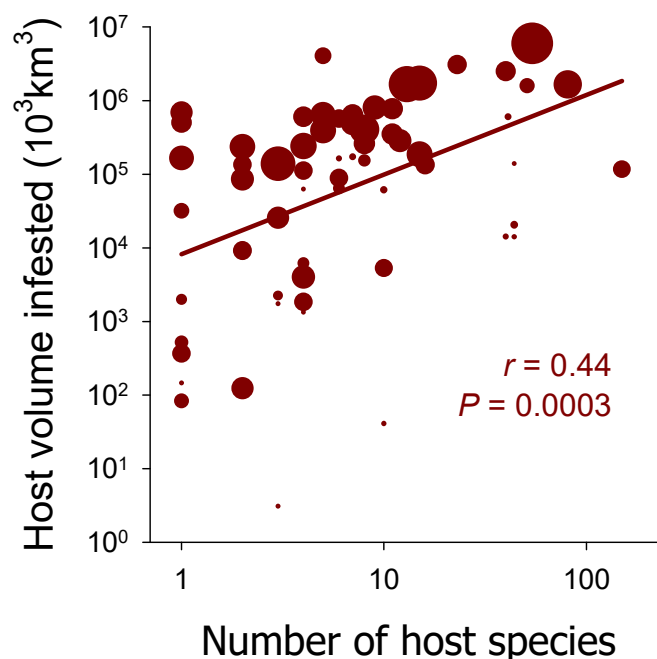
**Figure 1.** The specialist–generalist spectrum or continuum of host tree species for nonnative invasive pests across the United States forest ecosystems (the inserted panel shows the host frequency for the pests with  $\leq 20$  host species). Most of the 66 nonnative invasive pest species in the United States forests had a few host tree species.

Our specialist–generalist dichotomous comparison found that, on average, the tree volume infested by each pest species was lower among specialists than among generalists (Mann–Whitney Rank Sum Test,  $T = 797.00$ ,  $p < 0.001$ ; Figure 2A). However, the tree mortality caused by specialists (mostly pathogens, with 9 out of the 15 pest species causing significant tree death that were included in the analysis) was much higher than that caused by generalists (Mann–Whitney Rank Sum Test,  $T = 30.00$ ,  $p = 0.034$ ; Figure 2B). Among the 32 specialist nonnative pests, 9 species (28%) were among the top 15 that cause significant tree mortality, while among the 34 generalists, only 6 (18%) were among the 15 top pests.



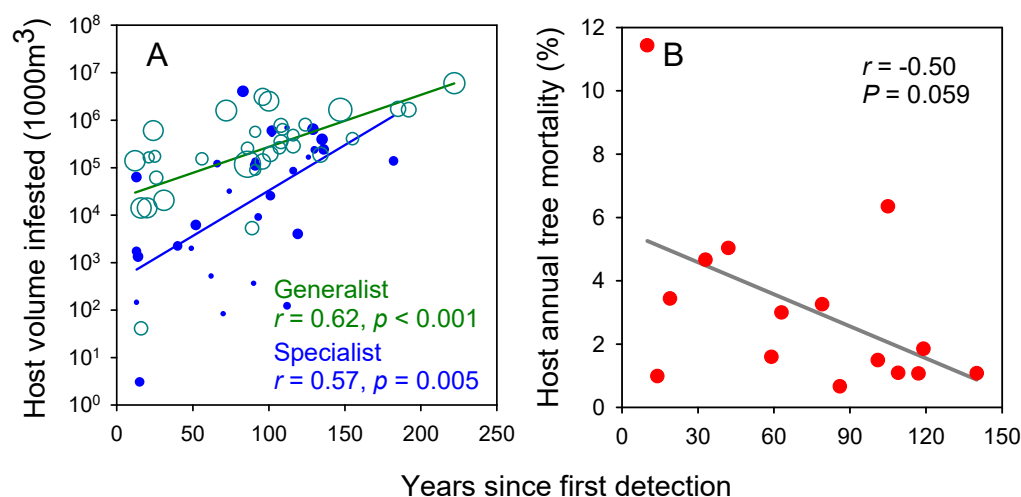
**Figure 2.** A comparison between the infestation volume (A) and mortality (B) in host trees caused by specialists v. generalists across United States forest ecosystems (the middle line in the box represents the median). Specialists lead to higher infestation ( $T = 797.00$ ,  $p < 0.001$ ), but the annual mortality rate shows the opposite ( $T = 30.00$ ,  $p = 0.034$ ).

When the specialist–generalist continuum concept was applied, i.e., using the number of host species as the independent variable (not a dichotomy), the infested host tree volumes increased with the number of host species (Figure 3).



**Figure 3.** Infested host tree volumes increased with the number of host tree species of nonnative pests across the US forests, assessed using the specialist–generalist continuum. Each dot represents a pest species (the symbol size reflects the years since the first detection). The figure shows infestation prevalence, a measure of the infection level that refers to the percentage of individuals in a population or group that are infested with a pest.

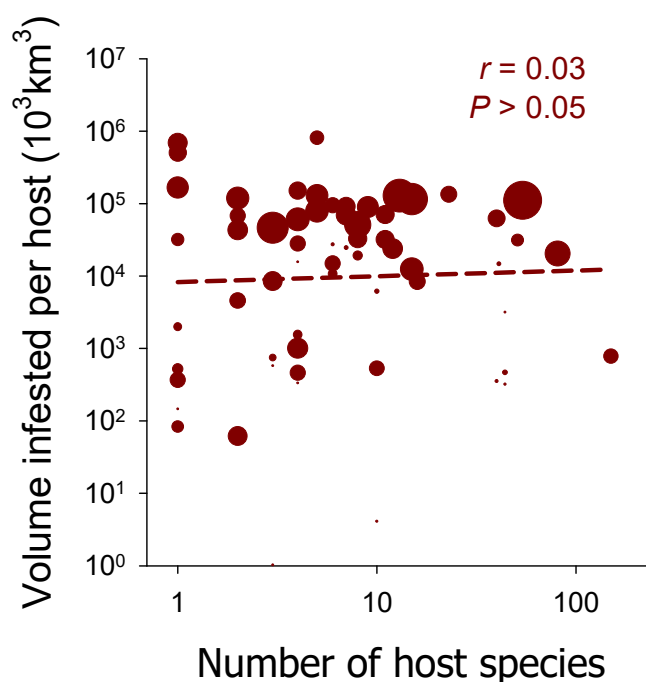
The infested host tree volumes also increased with the years since the first detection for both generalists and specialists, but at different rates (Figure 4A).



**Figure 4.** A comparison of the relationships of time (years since first detection) with host volume infestation (A) and the annual host tree mortality rate (B). In (A) there was no difference between the two regression slopes ( $T = 0.005$ ,  $p = 0.996$ ). Each symbol is a species (a total of 66 species) and the symbol size reflects host richness. In (B), the annual host tree mortality rate declines with time. Each symbol represents one of the 15 species with tree mortality data.

However, in contrast with expectations and counterintuitively, the annual host tree mortality rate (%) declined over time (years since first detection) ( $r = -0.50$ ,  $p = 0.059$ ; Figure 4B), although the total biomass infested still increased with time ( $r = 0.58$ ,  $p = 0.023$ , Figure S1).

Although the relationship between the time after first pest detection and the host volume infested by nonnative pests was stronger for specialists than for generalists, there was no significant difference between the two groups in their time-infested volume regression slopes ( $T = 1.17$ ,  $df = 61$ ,  $p = 0.245$ ; Figure 4). Furthermore, although generalists generally led to greater infestation on their host tree volumes than specialists (Figures 2A and 3), on average, a specialist pest did not cause more damage to each of its host species than a generalist (Figure 5).



**Figure 5.** No significant relationship existed between host tree richness and the tree volume infested for each host species across the United States forest ecosystems following the “specialist-generalist continuum” concept. The symbol size reflects the years since the first detection.

No significant difference was detected in both the host volume infested and the host tree mortality rate between pathogens and insects ( $T = 44.00$ ,  $p = 0.132$  and  $T = 43.00$ ,  $p = 0.556$ , respectively).

#### 4. Discussion

While it is expected that generalist pests cause high tree infestation, the most important finding from this study is that specialists cause significantly higher host mortality than generalists. Additionally, newly introduced nonnative pests lead to higher mortality rates than older invaders, which also is surprising. The most important reason that specialist pests cause greater host tree mortality could be that they effectively target only a few specific hosts so that on average, the individual host trees suffer much more than hosts targeted by generalist pests, which on average cause less damage to each individual tree across a broad set of hosts. Time is an important factor because the damage and damage type to pest hosts (loss of biomass vs. mortality) depended on the time since infestation and the host age (seedlings vs. old trees) [23]. The reasons for the higher host tree mortality by newer, nonnative pests may include the following: (1) nonnative pests that have been

around longer kill off the most susceptible host trees, resulting in the declining mortality of host trees over time; (2) pests that have been around longer spread to affect larger areas, and hence affect more volume/biomass (see the positive relationship between the invasion time and range size in Figure S2); and (3) the host tree species have time to adapt via natural selection to pests that have been around longer. All these explanations are possible as the mortality rate and infested volume data are from a single sampling year by the FIA, i.e., they are not the accumulative total mortality or infested biomass/volume since pest invasion.

Community-level studies on forest pest invasion in the United States have mostly been examined using richness data from both native trees and pest species. More recent studies have examined pest distributions across the US [5,13], overall pest damage on native trees or biomass loss due to pest invasions [2], and the role of native tree diversity in pest invasions [11]. The infested host tree volumes and host tree mortality in relation to pest specialization have rarely been investigated in terms of host selection. Our findings from this study shed new light on host specialization and on the relative damage (host tree infestation vs. mortality) assessed using the specialist–generalist continuum.

Because the total host tree volume (infested plus un-infested) is likely to increase with host richness, the infested volume is also expected to increase with host richness (Figure 3). It is still uncertain whether the two groups of species, specialists and generalists, may have a similar potential for further infestation in the future. However, it is possible that, on average, specialists cause more damage to their hosts, although this is difficult to prove as a host species may be attacked by multiple pests, including specialists and generalists. Nevertheless, some specialists indeed cause high host mortality [24], a consequence that deserves more urgent attention in future studies. The highest tree mortality-causing specialists in the United States include chestnut blight (*Cryphonectria parasitica* (Murrill) M.E.Barr) and hemlock woolly adelgid (HWA; *Adelges tsugae* Annand), as seen in [25,26]. On the other hand, some specialists that target certain plants have been used as biocontrol agents. For example, the flea beetle (*Aphthona* spp.) has been successfully used to control leafy spurge (*Euphorbia esula* L.), a highly invasive plant in some parts of the northern Great Plains [27].

In addition, some pests may not have reached their full, potentially suitable habitats, even though it has been more than 100 years since their initial detection. Furthermore, because many pests and their hosts have different favorable habitat conditions, their distribution (i.e., location and range size) do not always overlap, but changing climate conditions may allow for more overlap of host and pest environmental conditions in the future [17].

Studies to date show that specialists tend to evolve better in homogeneous environments with lower plant diversity, while generalists tend to evolve better in heterogeneous but species-rich habitats [28]. On the other hand, forest fragmentation or reduced forest area may generally favor generalist pests while presenting more risk to specialist pests in terms of pest richness [29,30]. For example, specialist insects and pathogens are more sensitive to fragmentation and edge types than generalist pests [31]. If further confirmed, this observation would have significant management implications.

Host generalism (species using multiple hosts) has previously been regarded as a hedge against shocks or extreme environmental changes [32]. Given enough time after invasion, the pest community composition depends on the host community composition (e.g., in terms of species diversity). In the real world, whether a specialist or a generalist pest has advantages over the other may depend on the changing dynamics in both the host and other pest community compositions; that is, in a system that already has more generalists, being a specialist may have advantages, and vice versa.

There are multiple challenges in pest monitoring, research, and management ahead [33,34]. Particularly, there is no standard approach to differentiating specialists vs. generalists. For example, there is no consensus regarding the taxonomic level (family, genus, or species) at which the number of hosts should be used to separate generalists and specialists. Even if the level is determined, we need to decide how many hosts (e.g., one vs. five) should be used as the criterion for defining a specialist (vs. a generalist). Also, as we show, using different measures to quantify tree damage (e.g., the total volume infested vs. tree mortality) leads to different conclusions about generalist and specialist impacts on their hosts. Finally, information regarding pest behavior and pest hosts in nonnative pests' native regions is critically needed to explain current infestations and predict future spread across their invaded forests under a changing climate [35]. Closer international collaborations are necessary to accomplish this [36].

## 5. Conclusions

Whether specialist pests cause more ecological damage is a complex issue, and the outcomes could vary depending on how we measure the damage and ecological and biogeographical contexts (locality, time, etc.). Since there is no consensus on how we define “specialist vs. generalist” and since how we assess forest damage (absolute vs. relative volume loss) can affect results, using the specialist–generalist continuum could be a more effective approach to assess their respective damage to forests. Since the impact of future pest invasions will also depend on how forest (interior) conditions may vary under the pressures from both climate and land use changes [31,37–39], monitoring the dynamic changes in the specialist–generalist continuum would be necessary. Findings from various comparisons along the pest richness “continuum” would be insightful for both basic biology and pest monitoring and management. Further studies on other related aspects, such as whether specialist pests spread faster than generalist pests or vice versa, also would be very useful [40].

**Supplementary Materials:** The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/f16010127/s1>, Figure S1: The host biomass infested by the 15 species with host tree mortality data increases over time; Figure S2: The positive relationship between time (years after first detection) and pest range size for the 15 nonnative pest species with host mortality data; Table S1: List of the 66 nonnative forest pest species known to cause significant damage to forest trees (hosts) in the United States. The rank of species only included the 15 species that cause significant host tree mortality.

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**Conflicts of Interest:** The authors declare no conflicts of interest.

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