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Predicting non-native insect impact: focusing on the trees to see the forest

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Abstract Non-native organisms have invaded novel ecosystems for centuries, yet we have only a limited understanding of why their impacts vary widely from minor to severe. Predicting the impact of non-established or newly detected species could help focus biosecurity measures on species with the highest potential to cause widespread damage. However, predictive models require an understanding of

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USDA Forest Service, Northern Research Station, 51 Mill Pond Rd., Hamden, CT 06514, USA potential drivers of impact and the appropriate level at which these drivers should be evaluated. Here, we used non-native, specialist herbivorous insects of forest ecosystems to test which factors drive impact and if there were differences based on whether they used woody angiosperms or conifers as hosts. We identified convergent and divergent patterns between the two host types indicating fundamental similarities and differences in their interactions with non-native insects. Evolutionary divergence time between native and novel hosts was a significant driver of insect impact for both host types but was modulated by

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A. M. Liebhold USDA Forest Service, Northern Research Station, 180 Canfield St., Morgantown, WV 26505, USA different factors in the two systems. Beetles in the subfamily Scolytinae posed the highest risk to woody angiosperms, and different host traits influenced impact of specialists on conifers and woody angiosperms. Tree wood density was a significant predictor of host impact for woody angiosperms with intermediate densities (0.5–0.6 mg/mm³) associated with highest risk, whereas risk of impact was highest for conifers that coupled shade tolerance with drought intolerance. These results underscore the importance of identifying the relevant levels of biological organization and ecological interactions needed to develop accurate risk models for species that may arrive in novel ecosystems.

Keywords Evolutionary history \cdot Forest pests \cdot Nonnative insect \cdot Risk assessment \cdot Scolytines \cdot Specialist insects

Introduction

The ability to identify which non-native species will cause ecological and/or economic damage prior to their arrival in a novel range is a central objective of invasion science (Foucaud et al. 2020). Although regulations for commodities have resulted in some

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Department of Agronomy and Horticulture, Center for Resilience in Agricultural Working Landscapes, School of Natural Resources, University of Nebraska-Lincoln, 3310 Holdrege Street, Lincoln, NE 68583, USA reductions in live non-native species transportation and introduction, new non-native species continue to be intercepted at ports-of-entry (Haack et al. 2014) and cause profound negative ecological and economic impacts (Diagne et al. 2021). Stricter inspections and regulations of whole groups of commodities (e.g., wood packaging material) may provide more protection, but it is not always feasible to inspect and regulate all imported materials without significantly increasing costs or reducing efficiency of trade facilitation. Accurate a priori assessment of risk could guide management efforts at the onset of, or even prior to, establishment of a non-native species, which could increase efficiency of regulatory and other prevention strategies, and decrease costs of response efforts (Simberloff et al. 2013; Tobin et al. 2014). One approach for predicting the potential impact of a nonnative species should it establish in a novel environment is to analyze previous invasions to determine if there are traits or other factors that are associated with different levels of impact (Ricciardi et al. 2013; Mech et al. 2019). Thus far, traits of introduced species have not been strong predictors of impact (Pyšek et al. 2012). Narrowing the scope of non-native species and ecosystems studied could facilitate finding traits or other factors that have predictive value because, within taxa and ecosystems, biologically relevant commonalities could emerge that may be masked when analyzing broader groups.

Like other ecosystems, forests are vulnerable to biological invasions by non-native, herbivorous insects (Lovett et al. 2016; Liebhold et al. 2017). Although most insect invasions have little or no negative impact, a small subset causes extensive tree mortality (Fig. 1; Aukema et al. 2010; Kenis et al. 2017). Mech et al. (2019) developed and validated a predictive model for the impact of non-native insect herbivores that specialize on coniferous trees (hereafter, conifer specialists) based on simultaneous consideration of multiple biological traits and other factors that modulate insect-host interactions. They found that evolutionary divergence time between a non-native insect's native and novel hosts, life history traits of the novel host, and level of relatedness between the non-native insect and native insects that evolved with the novel host were more predictive of impact than were traits of the invading insect. The question remains, however, how much these

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Fig. 1 Mortality of white ash (*Fraxinus americana*) in Toledo, Ohio (USA) caused by emerald ash borer (*Agrilus planipennis*), a nonnative hardwood specialist. Photograph by Daniel A. Herms

conclusions can be generalized to other groups of forest insects.

Here, we analyze the traits and factors associated with the risk of impact of non-native insect herbivores that specialize on a single family of woody angiosperms (hereafter, hardwood specialists) and compare these variables with those associated with the impact of non-native conifer specialists. This study followed the methodology of Mech et al. (2019) by using a model selection approach to test whether the probability of high impact for hardwood specialists is a function of (A) traits of the insect (e.g., taxonomy, life history, feeding guild), (B) life history and physiological traits of the novel host, (C) evolutionary divergence time between the host(s) the insect evolved with in its native range and the novel host(s) in the invaded range, and/or (D) relatedness of the insect to native insects that evolved with the shared invaded-range host. We also used data previously collected for conifer specialists (Mech et al. 2020a) to compare the traits and factors associated with impacts of nonnative insects between conifer and hardwood systems. We hypothesized that the risk of high impact from non-native hardwood specialists would be driven by the evolutionary history of the insect-host system, as in conifers (Mech et al. 2019), but with key differences among other traits and factors based on physiological differences between the two host types. Because biological invasions are an explicitly geographical phenomena, we focus on a single region: North America.

Materials and methods

Hardwood specialists and insect traits

We identified 191 non-native insects that can be considered hardwood specialists in North America using published lists (Aukema et al. 2010; Yamanaka et al. 2015). Insect species had to meet strict criteria for inclusion as a hardwood specialist (i.e., only feed on hosts in a single hardwood family and that at least one of those hosts is native to North America) to maintain standardization (Mech et al. 2019). For example, if a non-native insect only fed on one family, but its host species were all not native to North America, we did not include the insect in our analysis. Also, insects native to North America that crossed a geographic or climatic barrier via human transport and now utilize a novel North American host (e.g., Pityophthorus juglandis Blackman) were considered non-native in this study. Lastly, insects that use herbaceous plants as alternate hosts while in their asexual reproductive stage, and only a single hardwood family in their sexual reproductive stage, were considered hardwood specialists (Table A1). It was not feasible to conduct extensive literature reviews to obtain data for all 191 species; therefore, a sample of 100 hardwood specialists was used in this study. The list of species first included all of the non-native hardwood specialists thought to be potentially high impact by Aukema et al. (2010) and/or the authors of this paper, and then stratified random sampling was conducted to reach 100 species that reflected the same proportion of insect orders and feeding guilds (Table A2).

Extensive literature and online searches were conducted from July 2017 to May 2020. Searches were initiated with literature databases, such as Google Scholar and Web of Science, to identify peer-reviewed literature for each insect. Search terms for each insect generally included the scientific name, common name, and/or previously accepted synonyms. More specific search terms, such as "host" or "generation", were added to find information regarding the specific traits and factors included in this study. Because the majority of peer-reviewed publications regarding non-native insects tend to focus on species that cause damage, or only specific aspects of their life history, searches for missing information and for lessknown species used general Google searches. These allowed us to find additional resources such as state or federal reports, and online databases [e.g., ScaleNet (García Morales et al. 2016), HOSTS Database of the World's Lepidopteran Hostplants (Robinson et al. 2010)]. If a resource provided the host genus, but not the species, searches continued until there was confirmation regarding which host species were native to North America. As one of the goals was to ensure the reproducibility of the data collection protocol rather than to test the accuracy of historical host records, all of the host species documented through the searches were included in the analyses. All hardwood specialist insect and host data, including the 390 references associated with the literature searches, are available in Mech et al. (2020b).

For each hardwood specialist, values and species for the following categories were collected: (A) insect traits, (B) highest level of plant damage reported, (C) North American woody hosts, and (D) native woody hosts. The impact of each species was rated on the same nine-point scale used for conifer specialists, which ranged from 1 (no documented impact) to 9 (functional host extinction) (Table A3). The ninepoint impact scale could not be used for the conifer specialist analysis due to a small sample size. To draw direct comparisons to the conifer specialist analysis, a binary variable was also used to distinguish between hardwood specialist insects that cause minor damage or individual host mortality (i.e., not high impact), and those that cause population- or regional-level host mortality (i.e., high impact) (Mech et al. 2019; Schulz et al. 2020). Insect species that were categorized as "1" on the nine-point impact scale (Table A3) were assumed to be, and included in the analysis as, "not high impact" due to the lack of documentation of any impacts on their hosts.

Overall, the seven insect traits that were evaluated for conifer specialists were also analyzed for hardwood specialists: feeding guild, voltinism, reproductive strategy, dispersal mechanism, whether an insect congener is native to North America, whether the insect is considered a pest in its native range, and the number of host genera the insect utilizes in its native range (Table A4, Mech et al. 2020b). We also considered whether the insect was in the subfamily Scolytinae (bark and ambrosia beetles) because, among other features of their biology, their close association with fungi has resulted in some symbionts being highly phytopathogenic in novel hosts (Smith and Hulcr 2015; Table A2). Because phytopathogenicity and impact are both post hoc measures and therefore confounded, we treated the a priori trait membership in Scolytinae rather than microbial association as the insect trait of analysis. In addition, special deliberation was made about whether to include both Scolytus species (S. schevyrewi and S. multistriatus) that vector the fungi responsible for Dutch elm disease (Ophiostoma novo-ulmi and O. ulmi) and attack the same North American hosts. Although both result in high impact on their elm hosts, the biology of their systems is very similar, and only one species generally impacts a particular tree due to competitive exclusion (Lee and Seybold 2010; Jacobi et al. 2013). To avoid overrepresentation by vectors of the Dutch elm disease pathogens within the limited set of high-impact insects, and because one species captures the relevant model data for both, we chose to be conservative in our analyses and treat them as one (hereafter, S. schevyrewi/multistriatus).

Host traits

Literature searches identified a total of 151 North American hardwood species (trees or shrubs) used as hosts by the 100 sampled non-native hardwood specialists, resulting in 292 insect-novel host pairs. Six host traits evaluated for conifer specialists (foliage texture, growth rate, drought tolerance, fire tolerance, shade tolerance, wood density; Mech et al. 2019, 2020a), plus two additional traits (ability to resprout and C:N ratio of the aboveground herbaceous material of the hardwood host) were analyzed for hardwood specialists (Table A5, Mech et al. 2020b). All host values were obtained from the USDA Plants Database (United States Department of Agriculture-Natural Resources Conservation Services 2016), except wood density (Miles and Smith 2009).

Evolutionary divergence times between native and novel hosts

Each insect-novel host pair was matched with each native host of the hardwood specialist creating a dataset of 1,733 triplets. Divergence time estimates (millions of years ago; mya) between novel and native hosts were found for each triplet using the most comprehensively dated supertree of seed plant relationships available ("ALLOTB" tree; Smith and Brown 2018), which combines taxa in GenBank with additional taxa and a backbone of relationships among major clades provided by version 9.1 of Open Tree of Life (Hinchliff et al. 2015). This full dataset was used to find the shortest divergence time for each of the 292 insect-host pairs, which were then \log_{10} -transformed. We evaluated both linear and quadratic relationships between log₁₀ divergence time and probability of high impact. Since there was an interaction between feeding guild and divergence time for conifer specialists (Mech et al. 2019), the interaction was tested for in our analysis. The phylogeny used for conifer specialists did not include angiosperms, so we re-calculated the shortest divergence times for conifer specialisthost pairs using the ALLOTB tree (Smith and Brown 2018) to allow for direct comparisons.

North American insects that evolved with the novel hosts

To identify the closest insect relative that evolved with each novel host that the non-native hardwood specialist is utilizing, a list of native insects was compiled for each respective hardwood host. We used the same eight resources as the conifer study (Furniss and Carolin 1977, Drooz 1985, Burns and Honkala 1990, Johnson and Lyon 1991, Wood and Bright 1992, Blackman and Eastop 1994, Robinson et al. 2010, Pickering 2011) plus ScaleNet (García Morales et al. 2016) to account for a gap in the data on scale insects found in the other resources. Hosts that did not have available data in the resources utilized, were not included in analyses. In addition, to avoid potential false negatives arising from hardwoods not well represented in the literature, all host species for which ten or fewer native insects were identified (n = 56hardwoods) were excluded, yielding 95 hosts and 93 hardwood specialists (n = 226 insect-host pairs). For each non-native, hardwood specialist insect-host pair, this list determined whether there was a North American insect relative in the same genus or family as the non-native hardwood specialist that uses the same host (Mech et al. 2020b).

Statistical analyses

All analyses were similar to those of the conifer study (Mech et al. 2019), which allowed for comparisons between hardwood and conifer specialist systems. Statistical analyses were performed using R v. 4.0.0 (R Core Team 2020). We used multimodel inference within an information theoretic framework to rank the 11 and 10 unique generalized linear models (GLM) for the insect traits and host traits datasets (Table 1; Burnham and Anderson 2003). Competing models were fit using the logit link function and ranked based on Akaike's Information Criterion adjusted for small sample size (AICc; Akaike 1973) using the glm (family = binomial) and *aictab* functions in the 'stats' and 'AICcmodavg' packages in R (Mazerolle 2019; R Core Team 2020). \triangle AICc was used to compare the best-supported model (AICc = 0.00) and other models, with Δ AICc scores ≤ 2.00 included in the confidence set for assessment. Each of the four categories of interest were treated as individual submodels to determine their influence individually and then combined into one composite model to determine their collective influence on the probability of the nonnative hardwood specialist causing high impact. The formula for the composite model was identical to that for conifer specialists (Mech et al. 2019), which averaged residuals of the significant submodels and added the overall proportion of high impact incidences among all 292 insect-host pairs (0.086) to that average for each insect-host pair.

The Blomberg's K index of phylogenetic signal (Blomberg et al. 2003) was calculated to determine whether the host trait values and evolutionary history between the native and novel hosts were correlated ($K \ge 1$) or random (K = 0) and therefore represent independent factors for composite model construction. The 'phylosig' function in the 'phytools' package in R (Revell 2012) was used to calculate K values for each

trait and to test against the null hypothesis of random distribution on the phylogeny using 1,000 randomizations of trait values. Binary and ordinal traits were coded as integers for calculating K. The ALLOTB tree (Smith and Brown 2018) was used, but only included host species that had available trait values (n = 121 hardwoods). Trait values were plotted on the phylogeny using the 'phylosignal' package in R (Keck et al. 2016).

To assess the proportion of variability explained by each submodel and the composite model, the Nagelkerke pseudo R² goodness-of-fit metric was calculated (Nagelkerke 1991) using the 'fmsb' package in R (Nakazawa 2019). A ten-fold cross-validation test (Fushiki 2011) was conducted on independent data by randomly subsetting the dataset into training (90%) and testing (10%) sets. We evaluated the ten-fold cross-validation results for each submodel using a receiver operator characteristic (ROC) curve analysis (Hanley and McNeil 1982) and calculated the area under the curve (AUC; Fielding and Bell 1997). AUC scores range from 0 to 1, with a score of 0.5 indicating predictive performance equivalent to random chance and 1 indicating perfect predictive ability. The AUC score for the composite model was generated with data used to parameterize the ten-fold cross-validation.

Results

Of the 191 non-native hardwood specialists, eight (4.2%) caused high impact on North American hardwoods: (A) goldspotted oak borer (Agrilus auroguttatus Schaeffer), (B) emerald ash borer (Agrilus planipennis Fairmaire), (C) beech scale (Cryptococcus fagisuga Lindinger), (D) walnut twig beetle (Pityophthorus juglandis), (E) viburnum leaf beetle (Pyrrhalta viburni Paykull), (F) erythrina gall wasp (Quadrastichus erythrinae Kim), (G) banded/ European elm bark beetle (Scolytus schevyrewi/multistriatus Semenov), and (H) redbay ambrosia beetle (Xyleborus glabratus Eichhoff) (Table A2). Most were beetles (Coleoptera; 75%), with one scale insect (Hemiptera; 12.5%) and one gall wasp (Hymenoptera; 12.5%). Of the hardwood specialists included in the analysis, 29% were categorized as a "1" on the ninepoint scale, which indicates that they had no documentation regarding their effect on hosts. Hardwoods were used as hosts by 1-14 non-native specialist

insects (Table A6), and each insect had 1-12 novel host species.

Being a scolytine best explains a specialist insect's impact on hardwoods

Of the 11 models compared, the confidence set predicting high impact as a function of insect traits consisted of the single scolytine model that received 74% of data support (Table 1a). Scolytines posed a greater risk to their hosts than non-scolytine species; all non-native hardwood specialist scolytines currently in North America have caused high impact. Out of the eight high-impact species, five (63%) were wood borers (insects that bore into the host and fed under the bark), among which three (P. juglandis, S. schevyrewi/multistriatus, and X. glabratus) were scolytines. The insect traits scolytine model had a moderate predictive performance ($R^2 = 0.35$, AUC = 0.68) (Fig. 2).

Wood density of the hardwood host moderately explains insect impact

Of the 151 North American hardwoods, 37% hosted more than one non-native hardwood specialist $(\bar{x} = 1.93 \text{ insect species per host; Table A6})$. The best supported model (100% data support) explaining high impact of hardwood specialists as a function of host traits contained only the single variable of wood density, which had a quadratic relationship (Table 1b, Fig. 3). If the novel hardwood host had a moderate wood density $(0.5-0.6 \text{ mg/mm}^3)$, there was an 11-12% chance it would experience high impact from

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| Table 1 Ranking of alternative models explaining variability in non-native hardwood specialist impact as a function of (A) non-native insect traits, (B) novel hardwood host traits, and (C) their closest North American insect relative on the same host tree species | Model | Κ | AICc | ΔAICc | W | | |
|---|---|---|--------|-------|------|--|--|
| | (A) Insect traits | | | | | | |
| | Scolytinae | 2 | 43.51 | 0.00 | 0.74 | | |
| | Feeding guild | 5 | 46.29 | 2.77 | 0.19 | | |
| | Voltinism + reproductive Strategy + dispersal | 4 | 48.60 | 5.08 | 0.06 | | |
| | Reproductive strategy | 2 | 51.86 | 8.35 | 0.01 | | |
| | Voltinism | 2 | 55.30 | 11.78 | 0.00 | | |
| | Number of Genera | 2 | 57.32 | 13.80 | 0.00 | | |
| | Null model | 1 | 57.79 | 14.28 | 0.00 | | |
| | Congener | 2 | 58.93 | 15.42 | 0.00 | | |
| | Pest status + number of Genera | 3 | 59.36 | 15.85 | 0.00 | | |
| | Dispersal | 2 | 59.54 | 16.02 | 0.00 | | |
| | Pest status | 2 | 59.59 | 16.08 | 0.00 | | |
| | (B) Host traits | | | | | | |
| Lower Akaike's Information Criterion adjusted for small sample size (AICc) scores and higher AICc weights (w) indicate a greater relative degree of support for the model from the data. K indicates the number of parameters in each model, and Δ AICc is used to facilitate comparisons between the best-supported model (AICc = 0.00) and other models. All models with Δ AICc scores ≤ 2.00 | Wood density | 2 | 109.44 | 0.00 | 1.00 | | |
| | C:N ratio + Growth rate | 5 | 130.14 | 20.70 | 0.00 | | |
| | Growth rate | 3 | 133.64 | 24.20 | 0.00 | | |
| | Foliage texture + growth rate | 5 | 134.77 | 25.33 | 0.00 | | |
| | Fire tolerance + drought tolerance | 7 | 135.55 | 26.11 | 0.00 | | |
| | C:N ratio | 3 | 141.99 | 32.55 | 0.00 | | |
| | Ability to resprout | 2 | 145.35 | 35.91 | 0.00 | | |
| | Foliage texture | 3 | 146.61 | 37.17 | 0.00 | | |
| | Shade tolerance + drought tolerance | 6 | 152.78 | 43.34 | 0.00 | | |
| | Null model | 1 | 172.70 | 63.26 | 0.00 | | |
| | (C) Insect relatedness | | | | | | |
| | Shared genus | 2 | 106.33 | 0.00 | 0.50 | | |
| | Null model | 1 | 107.01 | 0.69 | 0.36 | | |
| (bold font) were included in the confidence set | Shared family | 2 | 108.87 | 2.54 | 0.14 | | |

a hardwood specialist, but risk decreased to < 1% if the novel host had lower or higher wood density (Fig. 3). Overall, the host traits submodel exhibited moderate explanatory ability ($R^2 = 0.13$, AUC = 0.74; Fig. 2).

Divergence time between native and novel hardwood hosts moderately explains insect impact

There was no significant interaction between hardwood specialist insect feeding guild and host divergence time; thus, we examined the effect of divergence times with combined guilds. There was a significant quadratic relationship between risk of high impact and the shortest evolutionary divergence time between the native and novel hardwood hosts $(p < 0.01 \text{ for divergence time and divergence time}^2)$. The greatest probability of high impact was on a novel host that diverged from the native host ~ 6 to 16 mya (Fig. 4a). For native and novel hosts that diverged 9.5 mya, there was an \sim 18% chance the hardwood specialist will cause high impact, but that risk decreased to nearly zero for hardwood hosts more distantly or closely related (Fig. 4a). Overall, the host evolutionary history submodel had moderate explanatory performance ($R^2 = 0.16$, AUC = 0.76, Fig. 2).

When reevaluating the conifer specialist data (Mech et al. 2020a) using the ALLOTB phylogeny



Fig. 2 Receiving operator characteristic (ROC) plot with area under the curve (AUC) statistics for assessing the ability of the hardwood specialist models to differentiate high impact insect– host pairs from non-high impact pairs at different probability thresholds

(Smith and Brown 2018), there was a significant quadratic relationship between risk of high impact and the shortest evolutionary divergence time of the native and novel conifer host (p = 0.02 and p = 0.01 for)divergence time and divergence time², respectively), as there was for hardwood specialists. However, the interaction between feeding guild and divergence times reported in the conifer study (Mech et al. 2019) was no longer significant (all p > 0.70) with the shift to using the ALLOTB phylogeny (Smith and Brown 2018). The greatest probability of high impact for a conifer specialist was on a novel conifer host that diverged from the native host $\sim 2 \text{ to } 6 \text{ mya}$ (Fig. 4b). For native and novel hosts that diverged 3.8 mya, there was a 21% chance the conifer specialist in any guild will cause high impact, but that risk decreased to nearly 0% for more distantly or extremely closely related conifer hosts (Fig. 4b).

Impact of non-native specialist insects is not affected by relatedness to native insects on the shared North American hardwood host

The presence of a North American insect in the same genus or family as the hardwood specialist feeding on the shared North American host did not affect the probability of the hardwood specialist causing high impact, as the confidence set of the best supported models (Δ AICc score < 2) included the null model (Table 1c). Of the 14 high impact insect-host pairs, 50% had a congener present on the shared host.

Combination of submodels explains more than any individual submodel

All Blomberg K values testing the relationship between host trait values and divergence times between native and novel hosts were < 1(0.004–0.38 range; Fig. A1). This indicates a weak correlation and justified inclusion of both submodels (hardwood traits and host divergence times) in the composite model evaluation. The combination of the three strongly supported submodels (insect traits, host traits, and divergence times) increased the overall explanatory power of the composite model (AUC = 0.87) relative to any submodel (wood density, AUC = 0.74; host divergence time, AUC = 0.76; scolytine, AUC = 0.68; Fig. 2).



Fig. 3 Observed (dots) and predicted probability (line) of high impact based on the wood density (mg/mm^3) of the novel hardwood host (0 = not high impact, 1 = high impact). Points have been jittered so all observations are visible

Discussion

Predicting the impact that a non-native species will have in novel ecosystems is a long-standing challenge within invasion biology. We found that narrowing the taxonomic focus by evaluating hardwoods and conifers separately improved our ability to explain the probability that non-native specialist insects will inflict high impacts on novel tree hosts (Table 2). Comparisons between these host systems revealed important similarities and differences that may have otherwise been eclipsed if all non-native specialist insects were pooled.

The main similarity between hardwoods and conifers was the importance of host evolutionary history, with divergence time between native and novel hosts being a relatively strong predictor of high impact in both systems (Fig. 4). The probability that a non-native specialist would have high impact was greatest when the novel and native hosts diverged at an intermediate time and approached zero when the novel host was either more closely or distantly related to the native host. A novel host that has recently diverged from a native host may retain similar, phylogenetically conserved defenses of the native host that minimize impact of the introduced insect (Gilbert et al. 2015), but these targeted defenses could erode over evolutionary time (e.g., by selection for allocating limited resources toward growth or defenses against other more frequently encountered herbivores). This would increase the probability that the invading insect will have high impact as it colonizes the novel North American host in a defense-free space (Gandhi and Herms 2010; Desurmont et al. 2011). As evolutionary divergence times between the native and novel hosts increase, these plants may diverge genetically and physiologically to the point that preference for a novel host is reduced, and as a result, impact of herbivory is minimal (Gilbert et al. 2015).

When using the same phylogeny, the peak probability of high impact occurred with hosts more distantly related for hardwood (~ 9.5 mya) than for conifer specialists (~ 3.8 mya) (Fig. 4). The phylogenetic relationships in the ALLOTB tree (Smith and Brown 2018) are largely concordant with other phylogenies, but the divergence times are uniformly



Divergence time from nearest native host (mya)

Fig. 4 Observed (dots) and predicted probability (line) of high impact (0 = not high impact, 1 = high impact) based on host evolutionary divergence time (millions of years ago; mya) between **a** native and novel hardwood hosts and **b** native and

more recent than most other estimates (Kumar et al. 2017). Thus, these divergence times may be considered minimum ages between native and novel hosts, and estimated dates are likely to shift as comprehensive plant phylogenies become more robust. The reason for different probabilities of peak impact for divergence time between hardwoods and conifers (Fig. 4) could be due to the different feeding guilds that dominate each group. Among high impact conifer

novel conifer hosts. Divergence times were derived from the ALLOTB phylogeny (Smith and Brown 2018). Points have been jittered so all observations are visible

specialist insect-host pairs, 69% were sap-feeders and the remaining were folivores (Mech et al. 2020a). In contrast, 72% of the 25 high impact hardwood specialist insect-host pairs were wood borers, with folivores (16%), gall makers (8%), and sap-feeders (4%) representing the remaining insect-host pairs. Overall, the divergence time submodel had a similar level of explanatory power for impact on both conifers (folivores, AUC = 0.77; sap-feeders, AUC = 0.81; **Table 2** Comparison of factors associated with the impact ofnon-native hardwood specialist (this study) and coniferspecialist (Mech et al. 2019) insects. Goodness-of-fit for each

model was evaluated using the Nagelkerke R^2 and area under the curve (AUC) statistics

| Model | Hardwood specialists | Conifer specialists |
|--------------------------|--|---|
| Insect traits | Scolytinae | No insect trait was significant |
| \mathbb{R}^2 | 0.35 | - |
| AUC | 0.68 | - |
| Host traits | Wood density | Shade + drought tolerance |
| \mathbb{R}^2 | 0.13 | 0.19 |
| AUC | 0.74 | 0.58 |
| Host phylogeny | No significant interaction with feeding guild | Significant interaction with feeding guild (folivores and sap-feeders)* |
| \mathbb{R}^2 | 0.16 | 0.43 (folivores); 0.36 (sap) |
| AUC | 0.77 | 0.77 (folivores); 0.81 (sap) |
| North American congeners | Neither shared family or shared genus were significant | Shared genus |
| \mathbb{R}^2 | _ | 0.09 |
| AUC | _ | 0.51 |
| Composite | | |
| \mathbb{R}^2 | _ | 0.91 |
| AUC | 0.87 | 0.91 |

*No significant interaction with feeding guild was found when the ALLOTB phylogeny (Smith and Brown 2018) was used

Mech et al. 2019) and hardwoods (AUC = 0.76), which reinforces the importance of the evolutionary relationship between native and novel hosts in driving the impact of non-native specialist insects.

The insect traits model (AUC = 0.68; Fig. 2; Table A2) best explained which non-native hardwood specialists are likely to cause high impact, with scolytines having a higher probability of causing high impact than non-scolytines. No insect traits predicted impact for conifer specialists, although the interaction between feeding guild and divergence time was found to be significant with the phylogeny used in their initial analyses (Mech et al. 2019). The number of established non-native, wood borers, including scolytines, continues to increase globally, especially due to widespread transport through solid wood packing material (Haack 2006; Lovett et al. 2016). Although many insects are benign in their native region where they typically colonize dead or dying trees, some kill living trees in their novel range (Hulcr and Dunn 2011; Ramsfield 2016). Moreover, scolytines are generally associated with fungal symbionts, which can become pathogenic on non-adapted hosts, or can acquire local fungi following an introduction, thus forming new associations (Wingfield et al. 2010; Hulcr and Dunn 2011; Ramsfield 2016). When one or both organisms in the symbiosis are non-native, a naïve host may lack defenses sufficient to resist attack (Wingfield et al. 2016). This highlights the need for biosecurity measures to dually focus on non-native insects and their potential microbial associates (Lovett et al. 2016).

Globally, symbiotic relationships between wood borers and fungal pathogens have caused widespread host mortality. In North America, this relationship, as represented by the scolytine variable, resulted in high impact for non-native specialists of hardwoods but not conifers. All non-native, hardwood specialist wood borers associated with fungi (all of which were Scolytinae–Ophiostomatalea fungal associations) were high impact. Conversely, none of the conifer specialist scolytines (also with Ophiostomatalea associates; Kirkendall et al. 2015) were high impact (Mech et al. 2020a). Outside of North America, however, there are non-native, conifer specialist scolytinepathogen complexes that can cause impacts, particularly when in combination with drought (e.g., *Dendroctonus valens* – *Leptographium procerum* in China; Yan et al. 2005), as well as non-native pathogens in North America that can damage conifers (Jacobs et al. 2004).

The reasons underlying the strong association between host impact and non-native insect-fungal pathogen complexes associated with scolytines in hardwoods but not conifers are unknown. One possibility is that North American conifers are at least partially preadapted due to the highly competitive pressures exerted by native scolytines, which include more tree-killing species and undergo more extensive outbreaks than elsewhere (Raffa et al. 2015; Huang et al. 2019). Conversely, the lower exposure of hardwood hosts to outbreaking native scolytines (Ohmart 1989; Grégoire et al. 2015) may select for less preadaptation. Another contributing factor may be anatomical differences that better allow tree-to-tree belowground transmission of beetle-vectored phytopathogens in angiosperms (e.g., longer root tracheids, long vessels) than conifers (Sperry et al. 2006). As there are more scolytines associated with hardwoods than conifers globally (Kirkendall et al. 2015), there is a higher probability of introduction; however, this did not explain the differences we found between host types. Out of all non-native specialist scolytines in North America, 70% were conifer specialists.

The probability of high impact for both hardwood and conifer specialists was influenced by host traits relevant to host quality. However, the specific host traits differed, with wood density being most important for hardwood specialists while shade and drought tolerance levels were most important for conifer specialists (Table 2; Mech et al. 2019). Wood density is associated with a suite of physiological and structural traits, and it is often positively correlated with wind resistance, chemical defense investment, and longevity, and negatively correlated with growth rate (Loehle 1988). The wood density of most North American hardwood species ranges from 0.3 to 0.8 mg/mm³ (Miles and Smith 2009). We found that the species most at risk of experiencing high impact had an intermediate density of 0.5 to 0.6 mg/mm³ (Fig. 3). Perhaps fast growing, early successional hardwoods with lower wood density are better able to tolerate herbivory than hosts with intermediate wood density, while slow-growing, well-defended, longlived hardwoods with higher wood density are better able to resist them. In a temperate rainforest, interspecific variation in tolerance of tree seedlings to simulated herbivory was positively correlated with their growth rate (Gianoli and Salgado-Luarte 2017). Conversely, wood density was not significantly associated with impact of conifer specialists; conifers that were both shade tolerant and drought intolerant had the greatest risk of experiencing high impact (Mech et al. 2019).

The differing effect of wood density between conifer and hardwood specialists could also be due to differences in insect traits. Most high impact hardwood specialist-host pairs were wood borers (70%), with almost half (all scolytines) having disease associations. Hosts with lower wood density and rapid growth may be at lower risk of high impact than species with intermediate wood density because fast growth may contribute to rapid compartmentalization of infection and decay. This hypothesis requires testing as few studies have related tree growth rate to rate of compartmentalization. Several physiological tradeoffs in responses of trees to wounding and infection have been characterized (Morris et al. 2020), and rate of wound periderm formation was correlated with trunk diameter growth rate across a range of hardwood species (Neely 1988). Hosts with very high wood density may be at a lower risk because they possess high concentrations of constitutive stem defenses (Loehle 1988), which may inhibit pathogen infection (Pearce 1996; Larjavaara and Muller-Landau 2010). Conversely, hosts with moderate wood density experiencing high impact may lack defenses adequate to inhibit infection and/or may not grow fast enough to compartmentalize infection when it does occur.

The presence of a closely related insect (shared genus or family) on the North American host did not influence probability of high impact for hardwood specialists (Table 1c). Although the presence of a congener reduced the probability of high impact by conifer specialists, the performance of the individual submodel in differentiating high impact and non-high-impact events was essentially no better than random (AUC = 0.51; Mech et al. 2019). This suggests there may only be a minimal difference between non-native conifer and hardwood specialists in the role that insect relatedness performs as a determinant of impact. Further, these models depend entirely on available data. Insect association data were generally available for common hardwood hosts, but less widely available

for rarer hosts and those characterized as shrubs (e.g., *Rosa* spp.). For purposes of comparison, we followed the protocols used in the conifer specialist study (Mech et al. 2019) to compile native insect lists but recognize that additional information could improve our understanding of this relationship.

As non-native forest pests continue to devastate forest ecosystems, better predictive ability of potential risk for newly detected species is urgently needed. This study further increases our understanding of traits and factors that drive the widespread mortality of tree species in North American forests caused by a small minority of non-native, specialist insects. Evolutionary history had a particularly important role in predicting high impact, which likely reflects the intimate relationship between specialist herbivores and their hosts. Interestingly, the relative importance of specific drivers of high impact differed between insects feeding on conifers versus hardwoods, with some variation explained by unequal representation among feeding guilds of the high impact insects in each host group. We suggest that the long-sought objective of predicting impacts of non-native species may be facilitated by better partitioning the complex variation among groups of interacting native and novel species. Hence, we narrowed the focus of our analyses to the host-type level, rather than the forest as a whole (Smith et al. 2015), which revealed important invasion patterns. This study illustrates how narrowing the scope of the organisms and traits examined may be necessary to achieve the level of resolution needed to make more accurate predictions of impact for various systems and non-native organisms. Similar research on polyphagous insects is required for a more comprehensive understanding of drivers of host impact for non-native, herbivorous insects in forest ecosystems.

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Authors' contribution TDM, KAT, DAH, and PCT conceived the project. All authors contributed to the study design; AMM, AMH, NPH, ANS, TDM, KAT, RAH, and AML collected the study data; ANS, AMM, DRU, and NPH analyzed the data; all authors contributed to writing and editing the manuscript; all authors gave final approval for publication and agree to be held accountable for the work performed therein.

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Data availability Data supporting the results are archived in the U.S. Geological Survey ScienceBase-Catalog (Mech et al. 2020a, b).

Declarations

Conflict of interest We declare we have no competing interests.

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