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ARTICLE

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Phylogenetic risk assessment is robust for forecasting the impact of European insects on North American conifers

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Abstract

Some introduced species cause severe damage, although the majority have little impact. Robust predictions of which species are most likely to cause substantial impacts could focus efforts to mitigate those impacts or prevent certain invasions entirely. Introduced herbivorous insects can reduce crop yield, fundamentally alter natural and managed forest ecosystems, and are unique among invasive species in that they require certain host plants to succeed. Recent studies have demonstrated that understanding the evolutionary history of introduced herbivores and their host plants can provide robust predictions of impact. Specifically, divergence times between hosts in the native and introduced ranges of a nonnative insect can be used to predict the potential impact of the insect should it establish in a novel ecosystem. However, divergence time estimates vary among published phylogenetic datasets, making it crucial to understand if and how the choice of phylogeny affects prediction of impact. Here, we tested the robustness of impact prediction to variation in host phylogeny by using insects that feed on conifers and predicting the likelihood of high impact using four different published phylogenies. Our analyses ranked 62 insects that are not established in North America and 47 North American conifer species according to overall risk and vulnerability, respectively. We found that results were robust to the choice of phylogeny. Although published vascular plant phylogenies continue to be refined, our analysis indicates that those differences are not substantial enough to alter the predictions of invader impact. Our results can assist in focusing biosecurity programs for conifer pests and can be more generally applied to nonnative insects and their potential hosts by prioritizing surveillance for those insects most likely to be damaging invaders.

KEYWORDS
conifer, herbivore, invasive species, phylogeny, risk analysis

For affiliation refer to page 12

INTRODUCTION

Invasive species are critical drivers of biodiversity loss and changes in ecosystem function and services (Simberloff et al., 2013; Vilà et al., 2010), and they cause billions of dollars of ecological and economic damage annually (Bradshaw et al., 2016; Cuthbert et al., 2022). Predicting and reducing the consequences of invasion are some of the most urgent goals of ecology, yet establishing effective priorities is particularly challenging because most introduced species are relatively benign, with only a small proportion become damaging invaders (Bradshaw et al., 2016; Williamson & Fitter, 1996). The ability to identify which species have the potential to cause major ecological or economic harm would greatly assist in prioritizing limited biosecurity resources for surveillance and eradication (Tobin et al., 2014). This knowledge is especially beneficial prior to or during the early stages of invasion (i.e., transport, introduction, and early establishment) when returns on management investments are the greatest (Epanchin-Niell & Liebhold, 2015; Yokomizo et al., 2009).

Previous research has focused on identifying the traits of organisms that might predict their success as invaders (Catford et al., 2016; Jeschke & Strayer, 2006) and their impacts on invaded communities (Dick et al., 2017; Kumschick et al., 2015; Liebhold et al., 2016; Mack et al., 2000; Mech et al., 2019; Sofaer et al., 2018). A pattern that emerges from this work is that the impact of an invader depends upon the community it invades. While an interesting insight, diversity in both invader and invaded community traits, along with the individualistic nature of invader-invaded community interactions, makes it difficult to determine, a priori, which introduced species are likely to cause harm. Some of the most damaging invaders are parasites and pathogens, which can decimate the species that serve as their hosts. The complexities and potential impacts of host–pest relationships, such as those associated with nonnative herbivorous insects, warrant deeper exploration.

Substantial effort has been devoted to understanding and making predictions about all stages of the invasion process, particularly for nonnative insects. Past research has tested the ability to predict novel host associations between plants and herbivorous insects (Branco et al., 2015; Pearse et al., 2013; Pearse & Altermatt, 2013) and evaluated the robustness of association predictions to critical sources of uncertainty (Pearse & Altermatt, 2015). Other studies have tested the ability to predict invasion pathway success or arrival (e.g., Fletcher et al., 2016; Hulme, 2009), establishment and spread upon arrival (e.g., Gougherty & Davies, 2021; Hudgins et al., 2017; Palamara et al., 2016), and host colonization (e.g., Pearse & Hipp, 2009). These and related efforts demonstrate how a range of predictive approaches are likely necessary for capturing the entire picture of invasion, from the characteristics and associations of an organism in its native range to the damage caused in a novel area. Many of these studies as well as others (e.g., Desurmont et al., 2011; Gilbert et al., 2012; Pearse & Rosenheim, 2020; Robles-Fernández & Lira-Noriega, 2017) recognize that the reconstructing of evolutionary history is valuable for predictions regarding invasion processes.

One of the final, most salient aspects of the study of biological invasions is predicting impact following introduction, host utilization, establishment, and spread. For nonnative herbivorous insects on trees, insect impact depends upon how closely related hosts are in the introduced range to those in the insect's native range (Mech et al., 2019; Schulz et al., 2021). Relatedness of hosts can be measured through divergence times obtained from reconstructed phylogenies, but these time estimates vary among published phylogenetic datasets. Great strides have been made in using DNA sequence data to reconstruct the phylogeny of conifers (Leslie et al., 2018) and, indeed, all extant plant species (Smith & Brown, 2018). Although the relationships among species are similar among different phylogenetic studies, regardless of methodology, divergence time estimates often vary because of uncertainty about the choice and placement of fossils used for calibrating molecular dating (Gernandt et al., 2018; Sauquet & Magallón, 2018). It is, therefore, crucial to evaluate whether and how predictions of impact may shift according to the phylogenetic dataset used. Here, we tested the robustness of predictions of nonnative insect impact to variation in estimates of divergence time between native and novel host species. Specifically, we evaluated potential shifts in predictions of insect invader impact and host vulnerability.

METHODS

Overview

Here, we apply the model framework of Mech et al. (2019) to European conifer-specialist insects (herbivore species that only utilize coniferous [Order Pinales] tree hosts) that have not yet established in North America. To test the sensitivity of the model framework to the host phylogeny used, we compared model inputs (i.e., divergence time estimates) and outputs (i.e., predicted likelihoods of high-impact invasion) among four published host plant phylogenies: two molecular phylogenies that focused on conifers (Leslie et al., 2012, 2018), one from a comprehensive phylogeny of seed plants that combined molecular data with

taxonomic relationships (Smith & Brown, 2018), and one from the online resource, TimeTree, that distills the scientific consensus on the phylogeny and divergence times of global biodiversity by assembling estimates from the scientific literature into a global TimeTree of Life (http://www.timetree.org; Hedges et al., 2015; Kumar et al., 2017). To answer fundamental questions about trends associated with closely related evolutionary groups, we used predictions from the phylogeny with the most comprehensive species coverage, Smith and Brown (2018), to rank insect and tree species according to relative risk and vulnerability, respectively. Specifically, we: (1) created a list of 62 European insect species ("risk species"); (2) identified and compared divergence time estimates among the four phylogenetic datasets; (3) refit and validated the Mech et al. (2019) model using data from each of the four phylogenetic datasets; (4) compared predicted likelihoods of high-impact invasion for all risk species among the four phylogenetic datasets; and (5) used high-impact likelihood predictions from Smith and Brown (2018) to evaluate risk and vulnerability trends among insects and conifer hosts, respectively.

Risk species identification

Our study focused on conifer specialists associated with trees native to Europe due to the region's general climate similarity to North America and readily available data pertaining to insect traits and hosts. Although we focused on insects native to Europe, many were considered Eurasian as they had a broader Palearctic distribution that encompassed parts of Europe as well as Asia (Appendix S1). The first step in compiling the risk species list was examining the USDA Animal and Plant Health Inspection Service (APHIS) Prioritized Offshore Pest List, which consists of ~150 pest species previously deemed to be of greatest threat to United States agriculture (USDA APHIS, 2012). However, only 12 species on the APHIS list were considered conifer specialists from Europe, and they were not reflective of the nonnative conifer specialists currently established in North America. For example, 53% of the established nonnative conifer specialists in North America are sap-feeding hemipterans, but the APHIS list contained none. Because the majority of currently established conifer specialists in North America feed exclusively on hosts in Pinaceae (Mech et al., 2020), we expanded our risk species list by evaluating insects feeding on four common Pinaceae genera and species in Europe: *Abies alba* Miller, *Larix decidua* Miller, *Picea abies* (L.) Hermann Karsten, and *Pinus sylvestris* L. We used Smith and Roy (2008), which focuses on British insects but is considered representative of continental Europe, to determine some of the European insects associated with these four conifer species and to add conifer specialists not currently established in North America to the risk species list. This increased the number of insect species from 12 to 142. Finally, we selected a stratified random subset ($n = 62$) of the full risk species list, based on the composition (order and feeding guild) of currently established nonnative conifer specialists. For these 62 insect species, we then used published literature and online searches to determine their feeding guild and full native host list (Appendix S1). For consistency, we calculated predicted risks for the same 47 North American conifers included in the previous model formulation (Mech et al., 2019), with the data needed for the North American host traits and coevolved insect submodels obtained from Mech et al. (2020).

Comparison of phylogenetic dataset divergence time estimates

To determine the divergence times for each native–novel host pair, Mech et al. (2019) used Leslie et al. (2012), who inferred the phylogeny of approximately 80% of extant conifer species using DNA sequence data from two chloroplast genes (*matK*, *rbcl*) and two nuclear genes (*18S*, *PHYP*). The divergence times were calibrated with 16 points placed throughout the phylogeny that were assigned lognormal date ranges based on fossil evidence. Three species not represented in Leslie et al. (2012)—*Abies balsamea* (L.) Miller, *Pinus cembra* L., and *P. banksiana* Lambert—were placed in positions within their respective genera based on their positions in other published phylogenies (Gernandt et al., 2005; Parks et al., 2012; Xiang et al., 2015). Leslie et al. (2018) used similar methods as Leslie et al. (2012) but added additional taxa to include ~90% of extant conifer species, added new matK and rbcL sequences and excluded all PHYP sequences to improve the evenness of data across clades, and added more fossil calibration points for a total of 26 minimum divergence dates, including some new fossils placed within crown genera.

TimeTree (Hedges et al., 2015; Kumar et al., 2017) is a public, web-based resource that compiles available divergence times for all organisms derived from molecular sequence data. Dated phylogenies from the peer-reviewed literature are collected and synthesized for the user. The divergence times assigned to nodes are the mean of all estimates available in the literature for that node. For our analyses, we generated a dated phylogeny using the "TimeTree View" option of inputting a list of taxa, accessed on 14 June 2020. Smith and Brown (2018) reconstructed a dated phylogeny of 353,185 species of

seed plant taxa using DNA sequence data mined from GenBank and phylogenetic data from Open Tree of Life (Hinchliff et al., 2015). Hierarchical clustering analysis was first used to reconstruct phylogenies of major clades using the sequence data. The relationships among these clades and the incorporation of taxa without sequence data were then estimated using data from the Open Tree of Life project. Generally, species that were not represented with sequence data in GenBank were placed in a basal position in their respective genera. Divergence times were estimated using the penalized likelihood method in treePL (Sanderson, 2002; Smith & O'Meara, 2012). This tree was calibrated using 590 points derived from the phylogeny of Magallón et al. (2015), which was itself calibrated at 137 nodes using fossil data.

The shortest divergence time for all native–novel host pairs was found using each of the four phylogenies (Kumar et al., 2017; Leslie et al., 2012, 2018; Smith & Brown, 2018). We used Pearson's correlation coefficient naïve to compare model inputs (i.e., divergence time estimates) among the four different phylogenetic datasets.

Refitting and validation of the Mech et al. (2019) model

For each of the four phylogenetic datasets, we followed the approach of Mech et al. (2019), who developed a host relatedness submodel explaining variability in impact among 58 conifer-specialist species already established in North America. Each submodel was then combined with the host traits and insect relatedness submodels of Mech et al. (2019) to form a composite model, resulting in four total composite models. Like Mech et al. (2019) and Schulz et al. (2020), we defined high-impact invasions as those resulting in isolated, sporadic, extensive, or persistent tree mortality within populations or regionally, up to causing functional extinction of the host tree, and not-high-impact invasions as those that directly or indirectly cause only minor damage or mortality of individual trees. We chose this impact dichotomy to have a large enough sample of high-impact species and because no matter the timeline of introduction, documented tree mortality at the population level is a prerequisite to even greater impacts.

To develop the four host-relatedness submodels, we used logistic regression to test for a significant interaction between quadratic divergence time and insect guild with, $\alpha = 0.10$. If the interaction was significant, we used Akaike's information criterion (AIC), adjusted for small sample size (AIC_c), in an information theoretic (i.e., model selection) approach, to rank three competing submodels according to support in the data: (1) impact $\sim$ divergence time; (2) impact $\sim$ divergence time^2; and (3) impact ~ 1 (i.e., null model; no predictors). The same three models were compared for folivores, sap-feeders, and all feeding guilds combined. If the quadratic divergence time–insect guild interaction was not significant, we used AIC_c to compare the same three competing submodels for the "all guilds" dataset alone. If the null submodel received an AIC_c score within two of the best-supported submodel, it indicated that none of the models in the set were viable, at which point the submodel was excluded from further consideration and was not integrated into the composite model. In the event there was model-based uncertainty between linear divergence time and quadratic divergence time models, we selected the best-supported model instead of performing model averaging.

The pseudo R^2 goodness-of-fit metrics for each submodel were calculated using the Nagelkerke R^2 (Nagelkerke, 1991) calculation through the *fmsb* package in R (Nakazawa, 2021). We used 10-fold cross-validation to gauge the predictive ability of submodels with independent observations (i.e., data not used in model training), which involves randomly subsetting a dataset into 10% and 90% groups, estimating coefficient estimates with the 90%, making predictions of high impact with the 10%, evaluating predictive performance with the known values of the 10%, repeating the process nine more times, and averaging the results (Fushiki, 2011). Within 10-fold cross-validation, predictive performance was quantified with receiver operator characteristic (ROC) plots and area under the curve (AUC) statistics (Fielding & Bell, 1997), which indicated the degree to which submodels correctly assigned greater likelihoods of high-impact invasion to high-impact than low-impact invasion events. Although each submodel was validated with independent data, composite models were validated with the data used to parameterize it.

Comparison of model predictions among phylogenetic datasets

Each of the four composite models was used to predict the likelihood of high-impact invasion for all risk insect–novel host pairs ($n = 2914$). We used the inverse logit transformation to convert raw model outputs (i.e., logit values) to continuous probabilities between 0 and 1. We used Pearson's correlation coefficients to compare high-impact likelihood predictions among the four phylogenetic datasets. To convert continuous predictions of high-impact likelihood to either high-impact or not high-impact groups, we used a threshold of 0.08 because this was the observed proportion of currently established

conifer-specialist tree pairs that were high impact (Mech et al., 2019).

Risk and vulnerability ranking

For the 47 North American conifer species evaluated, we presented high-impact invasion likelihood predictions across the 2914 risk insect–novel host pairs with the model refit with divergence times derived from the phylogeny of Smith and Brown (2018). We selected this phylogeny after the predictions were shown to be robust to the choice of phylogeny (see "*Results*" below), because it is the most comprehensively dated super-tree of seed plant relationships available to date and can retrieve data on missing species from other resources. To visualize relative risk and vulnerability across all pairs of risk insect and novel hosts in our study, we aggregated predictions in a phylogenetically structured heatmap using the *heatmap.2* function in the *gplots* package in (R Core Team, 2020; Warnes et al., 2020), with insect and conifer species ordered along the plot axes according to their phylogenetic relationships derived from the Open Tree of Life using the *rotl* package in R (Michonneau et al., 2016).

We also used high-impact likelihood predictions to calculate and showcase the utility of the mean predicted likelihood of high-impact invasion (P_a) across our sampled insect risk species, which can be used to rank tree species from greatest to least vulnerability to this particular cluster of risk insects. We also calculated P_c, the probability of at least one high-impact event across all 47 conifer species, which can be used to rank insect risk species from most to least risky. To visualize risk and vulnerability across insect and conifer species, we used the *ggplot2* (Wickham, 2016) and *dplyr* (Wickham et al., 2020) packages in R to generate histograms of the counts of classes of high-impact invasion likelihood for each risk insect and conifer species, and ranked the histograms by P_c and P_a, respectively.

RESULTS

Comparison of phylogenetic dataset divergence time estimates

Native–novel host divergence time estimates among the four phylogenetic datasets used in the host-relatedness submodel refitting were strongly positively correlated (all pairs $r \geq 0.95$), with the same rank order among phylogenies (Table 1). When comparing the four datasets, the same native host was selected as the closest relative for 98.8% of the risk insect–novel host pairs. Hence, the Mech et al. (2019) predictive model, which is largely driven by the evolutionary history between an insect's native and novel hosts, can find similar patterns of shortest divergence times in the host-relatedness submodel when using four different robust phylogenetic datasets reconstructed using different methods and with different calibration schemes.

Model refitting and validation

The model refitting process resulted in different host-relatedness submodel variables among the four phylogenetic datasets. Through generalized linear models, we found significant ($p < 0.10$) interactions between quadratic divergence time and insect guild for the phylogenies of Leslie et al. (2012, 2018) and Kumar et al. (2017), but not Smith and Brown (2018) (Appendix S2: Table S1). Consequently, we developed separate folivore, sap-feeder, and all guilds host-relatedness submodels for the Leslie et al. (2012, 2018) and Kumar et al. (2017) phylogenetic datasets, and a single all guilds host-relatedness submodel for the Smith and Brown (2018) phylogenetic dataset. For the folivore, sap-feeder, and all guilds submodels of Leslie et al. (2012), the quadratic divergence time submodel received more support (i.e., lower AIC_c scores) than the linear divergence time or null submodels (Appendix S2: Table S2), with pseudo R^2 values (i.e., goodness-of-fit) of 0.433, 0.356, and 0.158, and AUC (i.e., cross-validation) values of 0.802, 0.791, and 0.674, respectively (Appendix S2: Table S3). For Kumar et al. (2017), the linear divergence time submodel was best supported for folivores ($r^2 = 0.462$; AUC = 0.840) and all guilds ($r^2 = 0.080$; AUC = 0.632), whereas the quadratic divergence time submodel was best supported for sap-feeders ($r^2 = 0.116$; AUC = 0.629) (Appendix S2: Tables S2 and S3). The model selection approach did not clearly indicate whether the linear or quadratic divergence time submodel was better-supported for the folivore ($\Delta AIC_c = 0.535$) and all guilds ($\Delta AIC_c = 1.560$) submodels of Leslie et al. (2018). However, given the implausibility of averaging linear and quadratic divergence time models, we identified the linear divergence time submodel as the top model for folivores ($r^2 = 0.259$; AUC = 0.765) and the quadratic divergence time submodel as the best model for all guilds ($r^2 = 0.124$; AUC = 0.645) (Appendix S2: Tables S2 and S3). The quadratic divergence time sap-feeder submodel ($r^2 = 0.357$; AUC = 0.777) was best supported for the Leslie et al. (2018) phylogeny (Appendix S2: Tables S2 and S3). Finally, the best-supported all guilds submodel for Smith and Brown (2018) was the quadratic divergence time submodel ($r^2 = 0.22$; AUC = 0.705) (Appendix S2: Tables S2 and S3).

Comparison of model predictions among phylogenetic datasets

Composite model predictions of high-impact invasion likelihood among the four phylogenies were moderately-to-strongly positively correlated (all $r = 0.71–0.88$; Table 2). Predicted probabilities of at least one high-impact invasion event following the introduction and establishment of the 62 insect risk species (P_c) were also moderately-to-strongly positively correlated ($r = 0.54–0.93$; Table 3). Among the 2914 predictions of risk insect–novel host pairs that had high-impact invasion likelihood with the four composite models, there were only 40 instances (1.37%) in which the risk predicted using one source phylogeny was high (>0.08) but low (<0.01) when using another source phylogeny. These cases were associated with 27 risk conifer-specialist insects and nine conifer hosts.

Risk and vulnerability rankings

We used high-impact likelihood predictions from the model refit with divergence times derived from the phylogeny of Smith and Brown (2018) to rank conifers and insects according to vulnerability (P_a; Figure 1) and risk (P_c; Figure 2), respectively, as well as display the 2914 high-impact invasion likelihood predictions in a heatmap (Figure 3). Of the 2914 risk species-novel host pairs examined, 302 (10.4%) had a predicted risk of high impact above our threshold of 0.08. These pairs included 41 risk species (66% of the insect species studied) and 20 North American conifers (41.7% of our sample conifers). Using the Smith and Brown (2018) phylogeny, values of P_c ranged from 0.94 to 0.07, with 14.5% ($n = 9$) of risk species displaying a $P_c \geq 0.90$ (Figure 2). Based on the species we assessed, the pine-tree lappet (*Dendrolimus pini* L.), with $P_c = 0.94$, had a 94% chance of resulting in a high-impact invasion event for at least one of the 47 North American conifer species. Alternatively, the risk of at least one high-impact invasion event for brown larch aphid (*Cinaria cuneomaculata* Del Guercio)—the insect species with the lowest P_c—was 7.3%. Among conifer species, values of P_a ranged from 0 to 0.019, with the mean predicted likelihood of high-impact invasion across all risk insect species being greatest for red spruce (*Picea rubens* Sargent) (Figure 1). Because we focused on specific European host species in Pinaceae to create our risk insect species list, it was not surprising that North American conifers in the same genera as the European

TABLE 1 Correlation matrix of shortest divergence time for the four phylogenies ($n = 2739$ insect–tree combinations).

Phylogenetic dataset	Leslie et al. (2012)	Kumar et al. (2017)	Leslie et al. (2018)	Smith and Brown (2018)
Leslie et al. (2012)	1.00	0.99	0.99	0.97
Kumar et al. (2017)		1.00	0.99	0.95
Leslie et al. (2018)			1.00	0.96
Smith and Brown (2018)				1.00

TABLE 2 Correlation matrix of composite model risk predictions from the four phylogenies ($n = 2914$ insect–tree combinations).

Phylogenetic dataset	Leslie et al. (2012)	Kumar et al. (2017)	Leslie et al. (2018)	Smith and Brown (2018)
Leslie et al. (2012)	1.00	0.88	0.86	0.85
Kumar et al. (2017)		1.00	0.78	0.71
Leslie et al. (2018)			1.00	0.79
Smith and Brown (2018)				1.00

TABLE 3 Correlation matrix of predicted probabilities of at least one high impact from the introduction of 62 different nonnative insect species.

Phylogenetic dataset	Leslie et al. (2012)	Kumar et al. (2017)	Leslie et al. (2018)	Smith and Brown (2018)
Leslie et al. (2012)	1.00	0.93	0.59	0.79
Kumar et al. (2017)		1.00	0.54	0.65
Leslie et al. (2018)			1.00	0.67
Smith and Brown (2018)				1.00

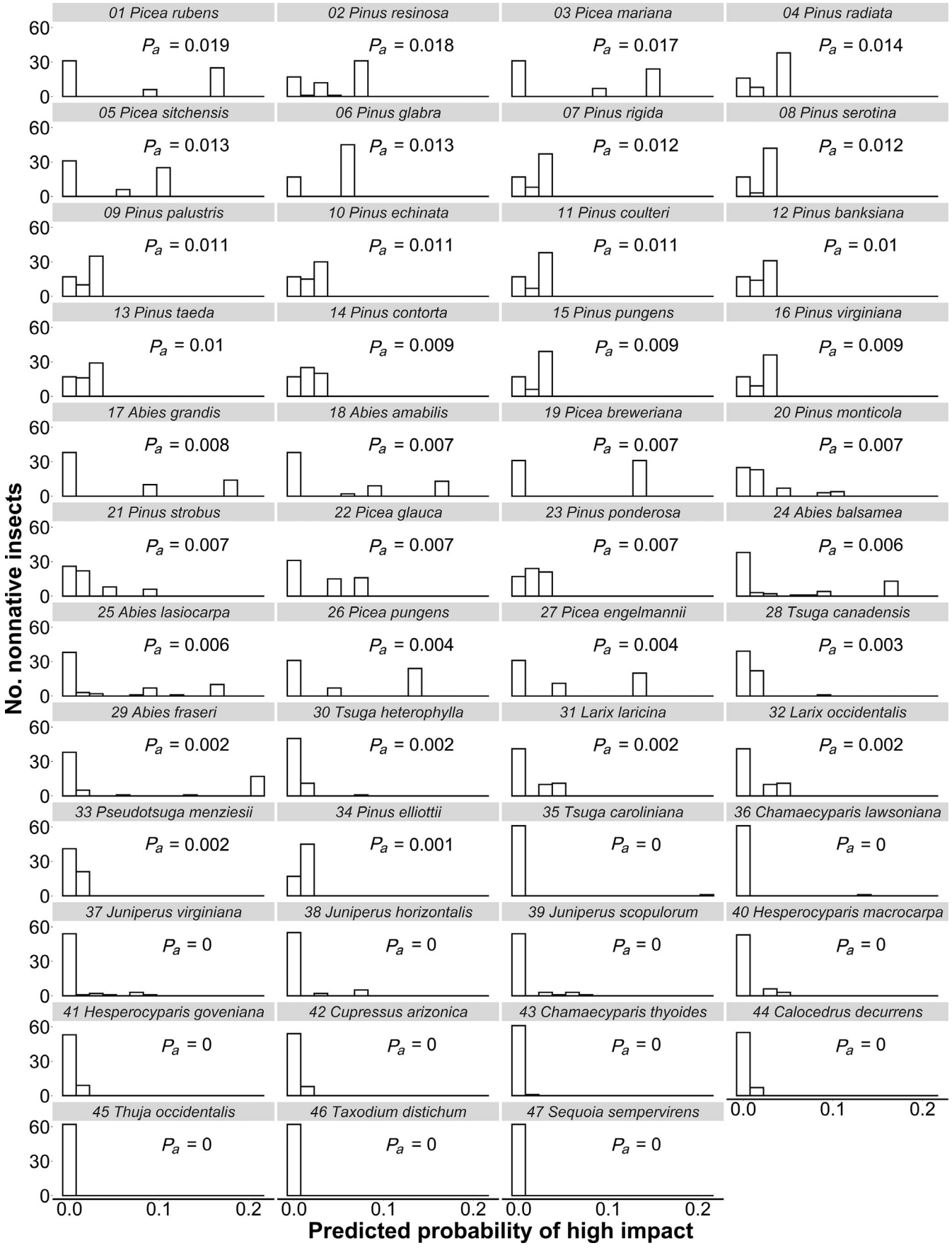

FIGURE 1 Legend on next page.

species (e.g., *Abies* and *Picea* spp.) were found to have relatively higher levels of vulnerability to high-impact invasion compared with species within Cupressaceae (Figure 3). Among the 62 insect species, risk of high-impact invasion was spread among insect orders, with relatively high levels of risk concentrated in Lepidoptera and Coleoptera. Overall, there were fewer predictions of high-impact invasion for the Hymenoptera and Hemiptera species included in our study (Figure 3).

DISCUSSION

Our results demonstrate that models fitted using information about previously established nonnative insects can be used to rank both the relative vulnerability of native host species (Figure 1) and the relative potential risk associated with insect species that have not yet arrived (Figure 2). Although prior studies have found that only a small proportion of nonnative species causes significant damage (Aukema et al., 2010; Williamson & Fitter, 1996), 66% of our stratified random sample of risk species were predicted to have a high probability of being high impact (>0.08) on at least one North American conifer should they become established. This difference highlights the importance of establishment in the invasion process, which our impact model does not predict.

Our comparison of model inputs and outputs when using different plant phylogenies (Kumar et al., 2017; Leslie et al., 2012, 2018; Smith & Brown, 2018) indicated that the selection of the specific plant phylogeny did not substantially alter risk predictions, in part because of the congruence in topology and divergence time estimates among phylogenies (Table 1), which is a testament to the current robustness of plant phylogenetic reconstruction. The phylogeny of Smith and Brown (2018) had notably shorter divergence times than the other source phylogenies, with the Pinaceae crown node dated to 71.7 million years ago (mya) versus 165.9–187.2 in the others, but these systematically shorter divergence times did not have a strong impact on the results. The predicted probabilities of at least one high-impact invasion for each conifer species across all 62 insect risk species (P_c) were more variable among phylogenies, but still displayed moderate-to-strong positive correlations (Table 3). Given the strong positive correlations among phylogenetic divergence time estimates, this increased variability in aggregated predictions was likely to be due to variation in the best-supported host-relatedness submodels (Appendix S2: Table S2). The agreement in predictions among models trained with divergence time estimates based upon different phylogenies lends confidence to the reliability of our model, as only 1.37% of the predictions differed in classifying a species as high impact or not high impact. These results complement similar efforts aimed at evaluating the robustness of model predictions about nonnative herbivorous insects at other stages along the invasion pathway (e.g., Pearse et al., 2013; Pearse & Altermatt, 2015).

In contrast with the null hypothesis of randomness in likelihood of high impact among the 2914 risk insect–novel host pairs, our results displayed clear phylogenetic patterns in both North American conifer species (i.e., columns) and nonnative conifer-specialist insects (i.e., rows) (Figure 3). Consistent with Mech et al. (2019), divergence time between native and novel hosts using Smith and Brown (2018) showed a quadratic relationship with the probability of risk, indicating that there is a "Goldilocks" region of high risk. If a North American conifer shared a common ancestor with the risk insect's native host ~2–10 mya, as opposed to <2 or >10 mya, it was predicted to be more vulnerable to a high-impact invasion by a conifer specialist. For the subset of insect species chosen for our study, North American fir (*Abies*) and spruce (*Picea*) were found to be more vulnerable to the introduction of European nonnative specialist insects that utilize fir and spruce in their native range. The most vulnerable tree that we found in our study was red spruce (*Picea rubens* Sarg.). The host traits submodel used in the Mech et al. (2019) composite model identified trees with the traits of high shade tolerance and low drought tolerance as being more vulnerable to high-impact invasions. In accordance with that study, North American fir and spruce bear these characteristics, whereas pine (*Pinus*) does not. The vulnerability of spruce and fir is also partially an artifact of our sampling method. Out of the 62 risk insect species evaluated, 30 utilized *Picea abies* (Appendix S1), a tree that has a paired divergence time with red spruce of 5.01 mya, right in the middle of the "Goldilocks zone" of high risk, further explaining the number of species in these genera with higher P_a values (Figure 1). Conversely, the selected European pine, *Pinus sylvestris* L., does not share a common ancestor in the

FIGURE 1 Histograms of the number of nonnative insects by predicted probability of high impact for each of the 47 North American conifer species. Conifer species are arranged by the highest mean predicted probability of high impact (P_a) (top left box, i.e., *Picea rubens* is the most likely to experience high impact from the European nonnative insects included in this study) to lowest mean probability of high impact (bottom right box, i.e., *Sequoia sempervirens* is the least likely to experience high impact from nonnative insects included in this study).

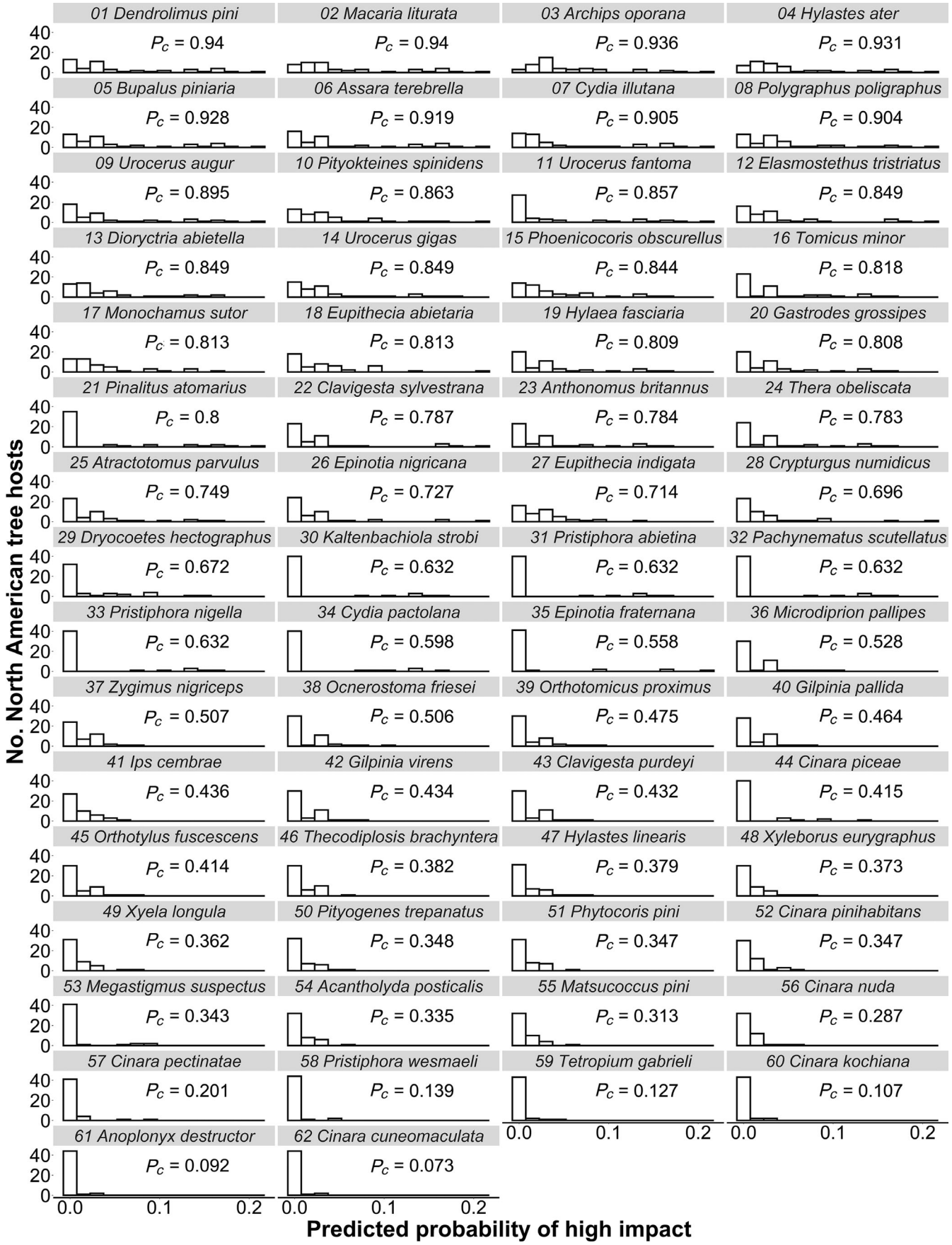

FIGURE 2 Legend on next page.

"Goldilocks" zone with the majority of North American pines. Thus, most of the pines on our list were not associated with many high predicted risks. One of the exceptions was red pine (*Pinus resinosa* Aiton), which shared a common ancestor with *Pinus sylvestris* 5.6 mya. This specific host pair also highlights the potential that the host-relatedness model may be symmetrical; that it could also apply to North American insects invading Europe. For example, the native hosts of the pine needle scale (*Chionaspis pinifoliae* Fitch) include red pine and white pine (*Pinus strobus* L.), but it can have a high impact on European trees planted in North America (Glynn & Herms, 2004), particularly those that have diverged from its native hosts in the "Goldilocks zone" of high risk (*Pinus sylvestris* and *P. mugo* Turra).

The ability to identify vulnerable tree species irrespective of a particular insect invader can inform invasive species biosecurity and management programs through the prioritization of limited monitoring resources to the most vulnerable tree species. The importance of host evolutionary history (i.e., shortest divergence time between native and novel hosts) in predicting the risk of high-impact invasions can be used to help to identify vulnerable North American tree species. Although other submodels incorporated within the composite model can influence the risk associated with specific insect species, the host-relatedness submodel identifies trends regardless of the insect associated with the host pairs. Using the phylogeny of Smith and Brown (2018), the "Goldilocks" zone of ~2–10 mya was associated with 197 native–novel host pairs. Within those pairs, 27 of the North American conifers included in our study (57.4%) had at least one data point in the high-risk zone. This indicates that there are certain tree species in other regions, such as Europe or Asia, that serve as a pool of potential high-risk insect species for at least one North American conifer species. A unique implication of this research is the ability to identify, for example, particular Palearctic trees that are within the high-impact "Goldilocks" zone of divergence times in relation to specific North American tree species, and then identify the insects that feed on those Palearctic trees to determine the species that would have the highest predicted risk of causing a high impact on those North American tree species.

Quantifying the risk of specific introduced insects to cause high impacts in North America can inform programs to prevent and manage biological invasions. Because of the high volume of global trade, it is not feasible for regulators to inspect all imported goods, find all insects contaminating goods, and prevent the introduction of all nonnative insect species (McCullough et al., 2006). Our results show considerable variation in the expected impact among nonnative European insects in North America (Figure 2). Specifically, knowledge of the insects most likely to cause high impacts, and the pathways through which they are most likely to enter, could inform mitigating actions. Strategic policy may decrease the likelihood of introduction and could be used to select high-risk tree species for targeted surveillance.

When jointly considering vulnerable conifer species and the predicted impact of a nonnative insect, this work could be extended by using the USDA Forest Service Forest Inventory and Analysis (FIA) program (McRoberts et al., 2005) to identify vulnerable biogeographic regions (or ecoregions) and vegetation communities that have relatively high-value tree species that might be at risk from introduced species. For example, Fraser fir (*Abies fraseri* (Pursh) Poir.) displays high levels of vulnerability across the 62 insect species, and Carolina hemlock (*Tsuga caroliniana* Engelm.) is highly vulnerable to one of our sampled nonnative insect species (Figure 3). Both of these conifers have a limited geographic range and ecological habitat, and hence a likely relatively narrow genetic pool, being restricted to the Great Smoky and Appalachian Mountains of Southeastern North America. Current surveillance for introduced species in the USA, such as the USDA Forest Service Early Detection and Rapid Response (EDRR) program (Rabaglia et al., 2019), targets specific insect species. While this approach certainly has merit, extending these programs by considering vulnerable ecoregions, vegetation communities, and species importance indicators (e.g., NatureServe Explorer plant community descriptions) could further help to prioritize the allocation of limited resources to biosecurity and invasive species management programs.

Although we have found confidence in the Mech et al. (2019) model to predict the risk of nonestablished conifer specialists in North America, we do not believe that this model should be used to make predictions about insects that feed on different host types (herbaceous plants or woody angiosperms) or that have a larger host breadth. Recent research has found that different drivers

FIGURE 2 Histograms of the number of North American conifers by predicted probability of high impact for each of the 62 nonnative European insect species. Insect species are arranged by the predicted probability of at least one North American conifer species experiencing high impact if all North American conifers were exposed to the insect (P_c) (top left box, i.e., *Dendrolimus pini* is most likely to be high impact on at least one North American conifer included in this study) to lowest probability of high impact (bottom right box, i.e., *Cinara cuneomaculata* is least likely to be high impact on at least one the North American conifers included in this study).

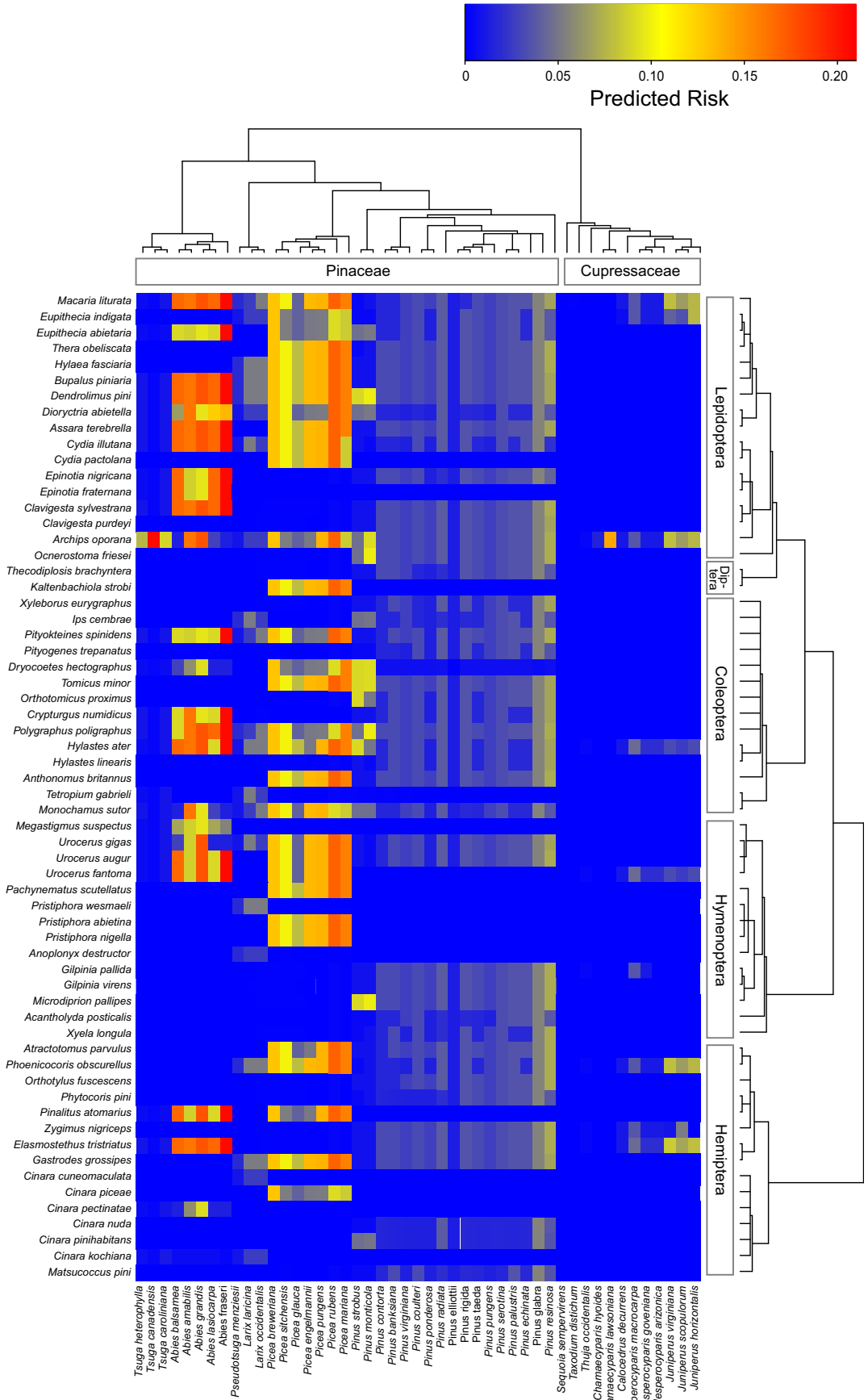

FIGURE 3 Legend on next page.

of impact may exist for other types of hosts, indicating that different risk models should be used for these variable groups (Schulz et al., 2021). However, based on our results, if host relatedness is a strong driver for other insect groups (woody angiosperm specialists or generalists), those model predictions will most likely also be robust, regardless of phylogeny used.

We were more likely to observe broad phylogenetic patterns among vulnerable hosts than among herbivores, as there were predicted high-impact risk species from all five insect orders included in our analyses (Figure 3). Nevertheless, our results can be used to identify specific risk insect–novel host pairs that have relatively high likelihoods of high-impact invasion. For example, our model indicates that the Fraser fir is particularly vulnerable, with 17 risk insect species predicted to have high likelihood of a high-impact invasion should they arrive and establish in North America (Figure 3). Last, our results can be used to differentiate between nonnative insects that pose a high risk to multiple conifer species and those predicted to negatively impact only a few conifer species. The comparison of our predictions of high-impact invasion likelihood to lists of known insect pests in the risk species' native range (e.g., those listed by the European and Mediterranean Plant Protection Organization [EPPO]), could be used to identify pest species that are likely to enter via invasion pathways.

The absence of a high likelihood of high-impact invasion for certain conifer species in our results does not mean that they are invulnerable. The insect species that we tested, and our focus on Europe as the source region, influences the conifer species identified as vulnerable. For example, not all species within Cupressaceae should be considered resistant to high-impact insect invasion, as might be suggested by the prediction matrix (Figure 3), because we did not include insects that feed primarily on members of Cupressaceae. In addition, our results only apply to the risk of invasion from Europe to North America. The distribution of divergence times among European and North American conifer species is expected to be different for other biogeographic regions. For example, conifer species in the Southern Hemisphere generally have older divergence times than those in the Northern Hemisphere (Leslie et al., 2012), and East Asia has higher conifer diversity than Europe (Farjon, 2010; Sundaram et al., 2019). These region-specific differences in host plant evolutionary history are likely to affect predictions of high-impact invasions, given the important role of evolutionary history (Mech et al., 2019). It is possible that certain low-risk areas in the prediction matrix (Figure 3) would be higher risk with broader geographic representation of nonnative insects. Therefore, we recommend that future research focus on how the patterns of risk to North American conifers differs for insects originating from other areas such as Asia or Latin America, both of which are major sources of species introductions in recent years due to global trade routes (Meurisse et al., 2019; Roques et al., 2020). Predicted risks could also be evaluated for insects that are commonly intercepted at ports of entry and therefore have high propagule pressure (Brockerhoff et al., 2014; Colautti et al., 2006). Overall, our study supports the increasingly illuminated role of native–novel host relatedness in determining an introduced insect's risk to new hosts and showcases that using different robust phylogenetic datasets to quantify this relatedness does not affect the resultant risks. Predictive models such as those used in this study can be used to mitigate future ecological and economic impacts in an increasingly connected world.

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FIGURE 3 Heatmap with the predicted risk of high impact of 62 European insects not yet established in North America (*y*-axis) on 47 conifer species native to North America (*x*-axis). Blue: insect–tree pairs represent a lower predicted probability; red: insect–tree pairs represent a higher predicted probability, of the nonnative insect having high impact on the North American conifer. Phylogenies show the relationships among the nonnative insect orders and among the North American conifer families, respectively. Risk values were derived using conifer divergence times from Smith and Brown (2018). For further information about the 62 European insects, see Appendix S1.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Mech et al., 2020) are available from the USGS at https://doi.org/10.5066/P9CLFQMI.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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