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What Is a Specialist? Quantifying Host Breadth Enables Impact Prediction for Invasive Herbivores

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Received: 21 March 2024 | **Revised:** 30 December 2024 | **Accepted:** 24 January 2025

Editor: Franck Courchamp

Funding: This project was conducted as a part of the 'High-Impact Insect Invasions' working group supported by the U.S. Department of Agriculture (USDA) Forest Service National Urban and Community Forestry Advisory Council Grant (Grant No. 19-DG-11132544-022 to RAH, DAH, and MPA), U.S. Geological Survey John Wesley Powell Center for Analysis and Synthesis (to KAT, TDM, DAH and PCT, and Cooperative Agreement No. G16AC00065 to PCT), and the USDA Forest Service Eastern Forest Environmental Threat Assessment (Grant No. 15-JV-11242303-103 to PCT). Additional support was provided by Colorado State University, National Science Foundation Long Term Ecological Research network (1637685, MPA), USDA Forest Service International Programs (MPA and AML), USDA National Institute of Food and Agriculture (Hatch project 1012868 to RAH, Hatch project ME022124 to AMM through the Maine Agricultural & Forest Experiment Station, and McIntire-Stennis project MISZ-069550 through the Forest and Wildlife Research Center to ANS), and U.S. Geological Survey Ecosystems Mission Area to KAT. PCT acknowledges support from the David R.M. Scott Endowed Professorship in Forest Resources. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Keywords: evolutionary history | generalists vs. specialists | herbivores | invasion risk assessment | phylogenetic diversity

ABSTRACT

Herbivores are commonly classified as host specialists or generalists for various purposes, yet the definitions of these terms, and their intermediates, are often imprecise and ambiguous. We quantified host breadth for 240 non-native, tree-feeding insects in North America using phylogenetic diversity. We demonstrated that a partitioning of host breadth: (1) causes 67% of non-native insects to shift from a generalist to specialist category, (2) displays a reduction in host breadth from the native to introduced range, (3) identifies an inflection point in a model predicting the likelihood of non-native insect ecological impact, with a corresponding change in behaviour associated with specialists versus generalists, and (4) enables three models for strong prediction of whether a non-native forest insect will cause high impacts. Together, these results highlight the primacy of how herbivore host recognition and plant defences mediate whether novel host interactions will result in high impact after invasion.

1 | Introduction

The concept of host breadth is both foundational to our basic understanding of plant–insect interactions and applicable to how to best contend with biological invasions. Categorising herbivores based on their host breadth is a common conceptual approach to develop ecological theory or predict herbivore behaviour. The specification of host breadth into categories, however, is commonly imprecise and ambiguous, limiting its utility. For example, specialised herbivores may be defined as species that utilise a single host plant species, genus, family or even up to a few families (monophagous or oligophagous) (Bernays and Graham 1988). Furthermore, different species that utilise the same number of plant genera or families may differ substantially in the range of underlying plant chemistry with which they contend because of divergent evolutionary histories among plant taxa.

The need for a more evolutionarily grounded definition for host breadth becomes heightened when evaluating novel interactions resulting from the introduction of non-native insect species, some of which can devastate forest ecosystems (Lovett et al. 2016). Novel plant–insect interactions often have tremendous negative influences on agricultural production, forest management and ecosystem services (Berenbaum and Zangerl 2008; Pearse and Rosenheim 2020). In North America, a small number of non-native, invasive tree pests, such as spongy moth [*Lymantria dispar dispar* (L.)], hemlock woolly adelgid (*Adelges tsugae* Annand) and emerald ash borer (*Agrilus planipennis* Fairmaire), have caused massive ecological and economic damage (Lovett et al. 2016; Fei et al. 2019). Models that predict impact risk for non-native insects that specialise on coniferous trees (Mech et al. 2019; Uden et al. 2023) or a single family of woody angiosperms (Schulz et al. 2021) have been developed; however, predicting the impact of species with broader host breadth has yet to be achieved. Part of the challenge impeding progress is the question of where to draw the line between host breadth categories. Strict host specialists are relatively easy to define, as are very broad generalists, but many species exhibit intermediate levels of specialisation. The specialist–generalist dichotomy remains useful because of physiological, behavioural and ecological differences between herbivores with narrow versus wide host breadths, especially regarding how they interact with their host plants (Bernays 1988). For example, extreme specialist insects typically develop targeted counter adaptations to particular host defences, whereas extreme generalists may be sensitive to those same defences (Ali and Agrawal 2012). What remains to be understood is how coevolved relationships of species interactions change along a continuum of specialisation, which is now more easily quantifiable due to the development of dated phylogenies for global plant species (e.g., Kumar et al. 2017; Leslie et al. 2012, 2018; Smith and Brown 2018).

The objectives of this study were to: (1) partition host breadth using phylogenetic diversity of hosts to establish a quantitative, unbiased boundary between narrow and wide host breadth for non-native, tree-feeding insect species in North America, (2) assess whether non-native insects increase or decrease their host breadth from their native to introduced range and (3) employ this host breath metric to predict the risk of impact of non-native insects on novel host trees. Though we used this new definition of host breadth to predict the impact that non-native insects have on novel hosts in North America, our approach to defining host breadth phylogenetically can be applied to address other fundamental questions about plant–insect interactions. For example, this same approach could be used to develop models that could predict the risk of impact for forest pests that invade other regions or evaluate the drivers of herbivores on herbaceous plants in North America. Other theoretical or practical applications that rely on defining host breadth could also benefit from incorporating a continuum of relatedness among hosts and quantitatively defining boundaries between categories.

2 | Materials and Methods

2.1 | Synthesis of Non-Native Insect Data

Two papers (Aukema et al. 2010; Yamanaka et al. 2015) were used to compile a comprehensive list of 508 non-native, herbivorous insect species that are established on native tree hosts in the United States and Canada. Two previously published databases included the traits and host information for 58 of the species categorised as non-native conifer specialists (only utilised conifer hosts; Mech, Thomas, et al. 2020) and for 100 non-native hardwood specialists (only utilised hosts in one hardwood family; Mech, Hoover, et al. 2020). This latter database included a representative subsample of the 191 total hardwood specialist species, as described in Schulz et al. (2021), with data documented in Mech, Hoover, et al. (2020).

For this study, we added to these databases by collecting information for non-native generalists (hosts in more than one tree family). It was not practical to include all 251 non-native generalists in the source list (Aukema et al. 2010; Yamanaka et al. 2015), so we sampled a stratified random set of 90 species with the same proportion of insect orders and feeding guilds as the original 251 species and with all of the high impact species included due to their low sample size. Data collection followed the same methodology as the other databases. Comprehensive searches of credible resources (e.g., books, journals, checklists and extension materials) were used to answer 54 questions per insect (see Schulz, Mech, Havill, Hoover, et al. 2024 metadata for details). Spongy moth had primary and secondary North American hosts documented, so we limited the list to primary hosts, as defined by Liebhold et al. (1995). In total, the three databases (Mech, Thomas, et al. 2020; Mech, Hoover, et al. 2020; Schulz, Mech, Havill, Hoover, et al. 2024) took over 5 years to create and included over 1000 references spanning over 150 years of research and observations (Figure S1). Eight insects that specialised only on shrubs were removed for this study, resulting in a subsample of 240 non-native tree-feeding insect species (47% of the 508 total) (Schulz, Mech, Havill, Hoover, et al. 2024).

The impact of the insects on each North American host tree was rated using a nine-point scale (Schulz et al. 2020) ranging from one (no documented impact) to nine (functional host extinction). These were then converted to a binary scale where species that caused impact only at the individual tree level (scores 1–5) were considered not-high-impact, and species that caused mortality at the host population level (scores 6–9) were considered high impact (Mech et al. 2019).

Insect and host traits were selected based on their potential to influence insect pest survival or reproduction, or host defensive capabilities, as determined by the literature on plant-insect interactions. Insect traits (Table S1; e.g., taxonomic family, feeding guild, native range, reproductive strategy) were synthesised from literature searches. North American host traits (Table S2; e.g., conifer or hardwood, drought tolerance, fire tolerance, foliage texture, growth rate, shade tolerance) were obtained from the USDA Plants database (USDA NRCS 2021), which had a higher representation of tree species and more complete list of traits than other sources, such as the TRY Database (Kattge et al. 2011). Wood density values were obtained from Miles and Smith (2009). Prior to modelling the insect and tree trait variables, correlation analyses were conducted to select representative traits that were not correlated (Mech et al. 2019).

After native and North American hosts lists for each non-native insect were collected, each insect-North American host pair was matched with each native host. Divergence time estimates (millions of years) between the novel and native hosts were estimated for each (insect-North American host-native range host) triplet. Uden et al. (2023) reported that the use of different phylogenies did not affect predictions of non-native insect impact on North American conifers. Therefore, we used the most complete supertree of seed plant relationships that is currently available ('GBOTB' tree; Smith and Brown 2018). This phylogeny was reconstructed using DNA sequence data from GenBank combined with taxonomic relationships provided by version 9.1 of Open Tree of Life (Hinchliff et al. 2015). All statistical analyses were performed using R v. 4.2.2 (R Core Team 2022). The R package V.PhyloMaker2 (Jin and Qian 2022) was used to generate a pruned GBOTB phylogeny, incorporating the host species for the insects in our data set. The 'cophenetic.phylo' function in the *ape* package (Paradis and Schliep 2019) in R was used to generate pairwise distances among hosts. The divergence time from each non-native host to the most recently diverged native host was selected for each of the 1627 insect–novel host pairs for the model. The synthesised trait and host data and the list of 1028 resources referenced for the data for the 240 insects were compiled into a single data set (Schulz, Mech, Havill, Hoover, et al. 2024).

2.2 | Quantification of Phylogenetic Host Breadth

Specialist and generalist herbivores are assumed to have different relationships with their respective hosts (e.g., different levels of susceptibility to host defensive compounds). Thus, we postulated that an unbiased delineation between these groups could be determined by evaluating how the sequential addition of more generalist insects altered the strength of the tree relatedness model previously found to be valuable for predicting impact of specialists (Mech et al. 2019; Schulz et al. 2021). We assigned each of the 240 non-native insect species along a host breadth continuum by calculating Faith's phylogenetic diversity (cumulative phylogenetic distance; Faith 1992; Tucker et al. 2017) of their native host tree species. Thus, an insect could be considered more of a specialist if it has a few closely related hosts, or more of a generalist if it has many distantly related hosts. For example, an insect that utilises multiple tree species in Betulaceae, Fagaceae and Juglandaceae might be typically categorised as a generalist, but these hosts are all in the Fagales clade, the members of which share many physical and chemical traits, suggesting that the insect may behave more like a specialist. We determined that phylogenetic diversity could provide additional information about the relationships between herbivores and their host plants compared to simply using host species richness (see Section 3).

Phylogenetic diversity was calculated with the R package *picante* (Kembel et al. 2010) using the divergence times estimated above. Since the input phylogeny is an ultrametric dated phylogeny, the phylogenetic diversity values are measured in cumulative millions of years (CMy). The tree relatedness model was repeatedly run using cumulative bins of 250 CMy. With each run, the predictive power of the model was determined based on the area under the curve (AUC) value. This continued until all 21 bins were included and then the AUC values were plotted with the corresponding CMy bins to identify the point where an increase in host breadth decreased the predictive power of the model. A sharp decline in predictive power was found at a phylogenetic diversity value of 2250 CMy (see Section 3), thus demonstrating a difference in response between insect species with a large host breadth ($\geq$2250 CMy) and those with a narrower host breadth ($<$2250 CMy). This cut-off was used to separate the non-native insect species into specialist versus generalist host breadth categories for all remaining analyses.

2.3 | Comparison of Native and North American Phylogenetic Host Breadth

We assessed the relationships between: (1) the number of native host species and native host phylogenetic diversity and (2) host phylogenetic diversity in the native and introduced ranges. Spearman's rank correlation coefficient was used to quantify the strength of these relationships. Relationships between host phylogenetic diversity in the native and introduced ranges were compared among native range biogeographic realms (e.g., Afrotropic, Australasia, Indomalaya, Neotropic and Palearctic) and insect feeding guild using a Kruskal–Wallis rank sum test to assess whether insects from different biogeographic realms or different feeding guilds had more or less hosts than they had in the introduced range.

2.4 | Development of Models to Predict Non-Native Insect Impact

To predict non-native insect impact for all insect species (specialists and generalists) on all host types (conifers and hardwoods), we evaluated three primary models: (1) insect traits, (2) tree traits and (3) tree relatedness. A multimodel inference within an information theoretic framework was used to rank the unique generalised linear models (GLM) within the insect traits and tree traits models (Burnham and Anderson 2003). For the tree relatedness model, we $\log_{10}$-transformed the shortest divergence time for each of the insect–host pairs, then evaluated both linear and quadratic relationships with each respective insect's probability of high impact. The logit link function was used to fit the competing models, which were 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, respectively (R Core Team 2022; Mazerolle 2019). The best-supported model (AICc = 0.00) was compared to the other models using ΔAICc. Any models with ΔAICc scores ≥ 2.00 were excluded from the final model. If the null model was within the top set of models, the model was considered insignificant.

Each primary model was assessed using the same methods as past studies using conifer and hardwood specialist insects (Mech et al. 2019; Schulz et al. 2021). Significant drivers from each primary model were combined into a composite model to determine the collective influence on the probability of the non-native insect causing high impact. Models without significant drivers were excluded from the composite model. To measure variation explained by each model, we calculated a Nagelkerke pseudo R^2 goodness-of-fit metric (Nagelkerke 1991) using the *fmsb* package in R (Nakazawa 2019). We then conducted a 10-fold cross-validation test (Fushiki 2011) by randomly subsetting the data set into training (90%) and testing (10%) sets. We evaluated cross-validation results for each model and the overall composite models using a receiver operator characteristic (ROC) curve analysis (Hanley and McNeil 1982). Area under the curve (AUC; Fielding and Bell 1997) scores, which range from 0 to 1, with a score of 0.5 indicating predictive performance equivalent to random chance and 1 indicating perfect predictive ability, were calculated for each primary model and composite model for each host breadth category. The data used to parameterise the 10-fold cross-validations were used to generate the AUC scores for the composite models.

Preliminary analyses using the full list of 240 non-native insects resulted in no strong, significant predictors within any of the three primary models tested, likely because of their biological variation associated with host breadth (Tables S3 and S4). Therefore, all subsequent analyses were partitioned by phylogenetic diversity (specialist < 2250 CMy and generalist ≥ 2250 CMy) to maximise model predictive ability. Additional splits (e.g., by feeding guild) would have likely resulted in fewer high-impact insects in each category and sample sizes too small for accurate predictions. No high-impact insects with a phylogenetic diversity ≥ 2250 CMy exclusively utilised conifers, so conifer hosts were excluded from the generalist model analyses to further refine the models. Data were, therefore, partitioned into three final categories: (1) conifer specialists ($n = 69$), (2) hardwood specialists ($n = 141$) and (3) generalists ($n = 30$) (Figure 1).

3 | Results

3.1 | Quantifying Phylogenetic Host Diversity

A sharp decline in predictive power of the model to predict non-native impact using tree relatedness between native and novel hosts was found at 2250 CMy (Figure 2A), thus providing a useful quantitative boundary between more specialist (< 2250 CMy) and more generalist (≥ 2250 CMy) insects (Figure 2B). The distribution of host tree phylogenetic diversity for 240 non-native forest insect species in North America did not have discrete peaks corresponding to 'specialists' and 'generalists' and was not linear with host species richness (Figure 2B). This new delineation resulted in 67% of non-native insects previously considered generalists (as commonly defined by utilising more than one plant family) to fall in the more specialised group, which now had 218 non-native insect species with an average host tree phylogenetic diversity value of 330 CMy (± 35 SE). Although the bulk of the insects in this group only utilised a single host family (69.3%), it now included some species that utilise more than one host family but behave more like specialists than generalists in the model. Comparatively, insects in the generalist category each utilised hosts in more than 13 tree families (maximum = 152 species in 48 families; average phylogenetic diversity of 4111 CMy ± 287; Figure 2B). Although we only used the primary hosts for spongy moth, it still had a high enough host breadth to remain a generalist species. The intermediate area of the phylogenetic diversity continuum (i.e., zone of higher variability, 1500–2500 CMy; Figure 2B), which spans our quantified delineation, represents a transition to resolve potential disagreements in customary host breadth categories (Figure 2A).

3.2 | Correlation Between Native and North American Host Phylogenetic Diversity

We found a positive correlation between native and North American host phylogenetic diversity, such that insects that utilised more hosts in their native range also tended to utilise more hosts in the introduced range, though often with a narrower host breadth in the introduced range (Figure 3A). Overall, approximately 30% of the insects increased host breadth, 5% had no change, and 65% reduced host breadth from their native range to North America, with 6.5% (16 species) decreasing their host breadth so much so that they went from being classified as a generalist in their native range to a specialist in North America. The mean (± SE) host phylogenetic diversity in the native range was 787.4 ± 90.9 CMy, compared to 477.1 ± 57.9 CMy in the introduced range. When we compared native versus novel host breadth, we found that insects from Asia had a large, albeit marginally significant ($n = 51$, $\chi^2 = 2.83$, $p = 0.09$) decrease in mean host phylogenetic diversity (Figure 3B). European species ($n = 134$, $\chi^2 = 5.08$, $p = 0.02$) and species that could be found across the broader Palearctic region ($n = 48$, $\chi^2 = 5.65$, $p = 0.02$) had a significant decrease, while species from other areas (Afrotropic, Australasia, Indomalaya and Neotropic; $n = 15$, $\chi^2 = 0.19$, $p = 0.66$) did not have a decrease in host phylogenetic diversity (Figure 3B). Comparisons by insect feeding guild showed that gall makers ($n = 13$, $\chi^2 = 6.14$, $p = 0.01$), sap feeders ($n = 120$, $\chi^2 = 4.34$, $p = 0.04$) and wood borers ($n = 35$, $\chi^2 = 4.75$, $p = 0.03$) had a significantly narrower host breadth in North America, whereas folivores ($n = 68$, $\chi^2 = 0.41$, $p = 0.52$), reproductive feeders ($n = 7$, $\chi^2 = 1.64$, $p = 0.20$) and root feeders ($n = 5$, $\chi^2 = 0.18$, $p = 0.68$) did not vary between the native and introduced ranges (Figure 3C).

3.3 | Host Breadth Delineation Permits Impact Prediction for any Non-Native Forest Herbivore

Separate models to predict high impact based on insect host breadth and host category yielded significant factors, indicating

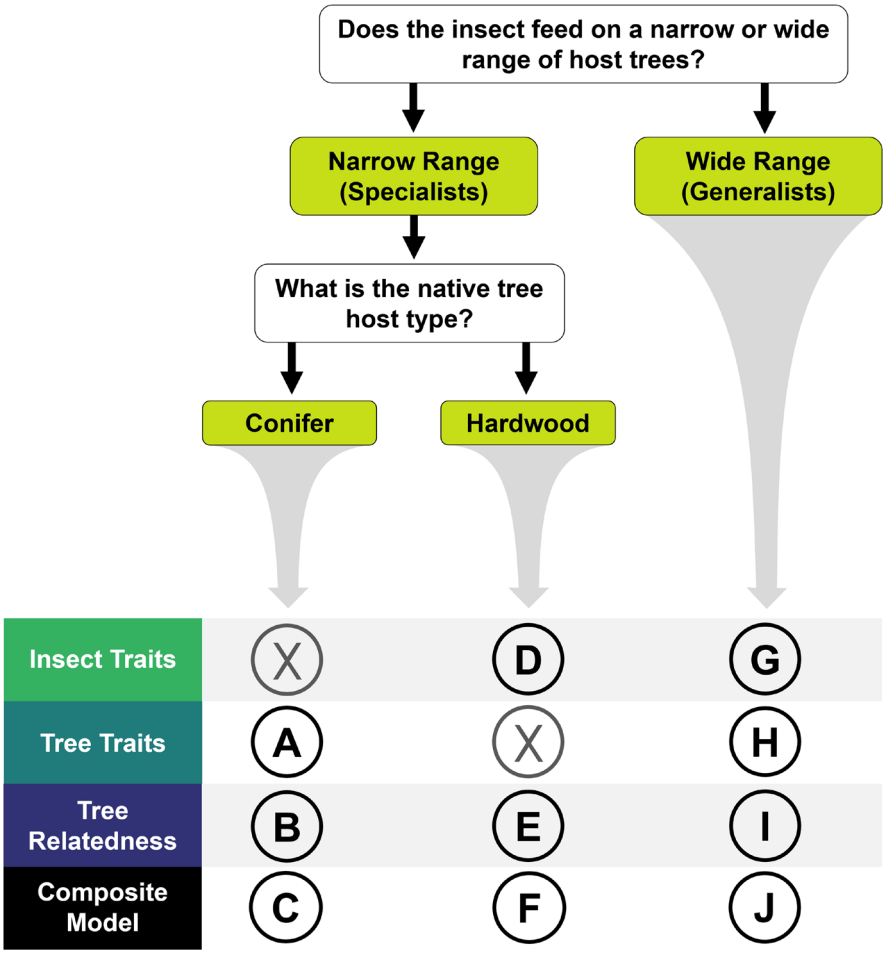

FIGURE 1 | Summary of the models developed to predict non-native forest insect impact. The three composite models developed in this study comprise up to three separate models [insect traits, tree traits and tree relatedness (divergence time between native and novel hosts)]. Composite model one for conifer-feeding insects with a narrow host range (phylogenetic diversity < 2250 CMy) is composed of the tree traits and tree relatedness models. Composite model two for hardwood-feeding insects with a narrow host range is composed of the insect traits and tree relatedness models. Composite model three for hardwood-feeding insects with a wide host range (phylogenetic diversity ≥ 2250 CMy) is composed of the insect traits, tree traits and tree relatedness models. Models that are not included in the associated composite model are denoted with a grey 'X'. All lettered models were included in the subsequent composite models and correspond to the letters in Figure 3.

the importance of these partitions compared to a single merged analysis. The separations resulted in three composite models: conifer specialists, hardwood specialists and hardwood generalists (Figure 1). Among insect traits, feeding guild was significant for hardwood specialists and generalists, but not for conifer specialists (Figures 1 and 4; Tables S5 and S6). The guild with the highest risk of impact also varied by host breadth category—wood borers were the riskiest within the hardwood specialist versus folivores within the generalist group (Figure 4D,G). Although sap feeders are a numerically dominant introduced group in North American forests (48% of species), they pose less risk of impact. Among host tree traits, shade tolerance was found to be significant for conifer specialists and generalists, but not hardwood specialists (Tables S7 and S8). Specifically, shade-tolerant conifers had a higher risk of high impact from conifer specialists (Figure 4A; Tables S7 and S8), whereas shade-tolerant hardwoods had a lower risk of high impact from generalist insects (Figure 4H; Tables S7 and S8).

Although host evolutionary history has been underappreciated in understanding the impact of non-native herbivorous insects, tree relatedness was the only significant primary model for all three host breadth categories (Figures 1 and 4; Tables S9 and S10). In all cases, we found a quadratic relationship between tree relatedness and insect impact risk, where native and North American host trees that were very closely or distantly related were less impacted than hosts that diverged somewhere in the middle (Figure 5). The greatest risk was to North American hosts that had diverged from the insect's native range hosts 3–4 million years ago for conifer specialists (Figure 4B), 5–9 million years ago for hardwood specialists (Figure 4E), and around 1–2 million years ago for generalists (Figure 4I). For each of the three host breadth categories, the merged composite model had stronger predictive ability than any of the individual significant primary models alone (Figure 4C,F,J; Table S11).

4 | Discussion

Specialist and generalist insect herbivores have distinct differences in their feeding behaviours and ecological functions that can influence their impacts on ecosystems (Bernays 1988). The

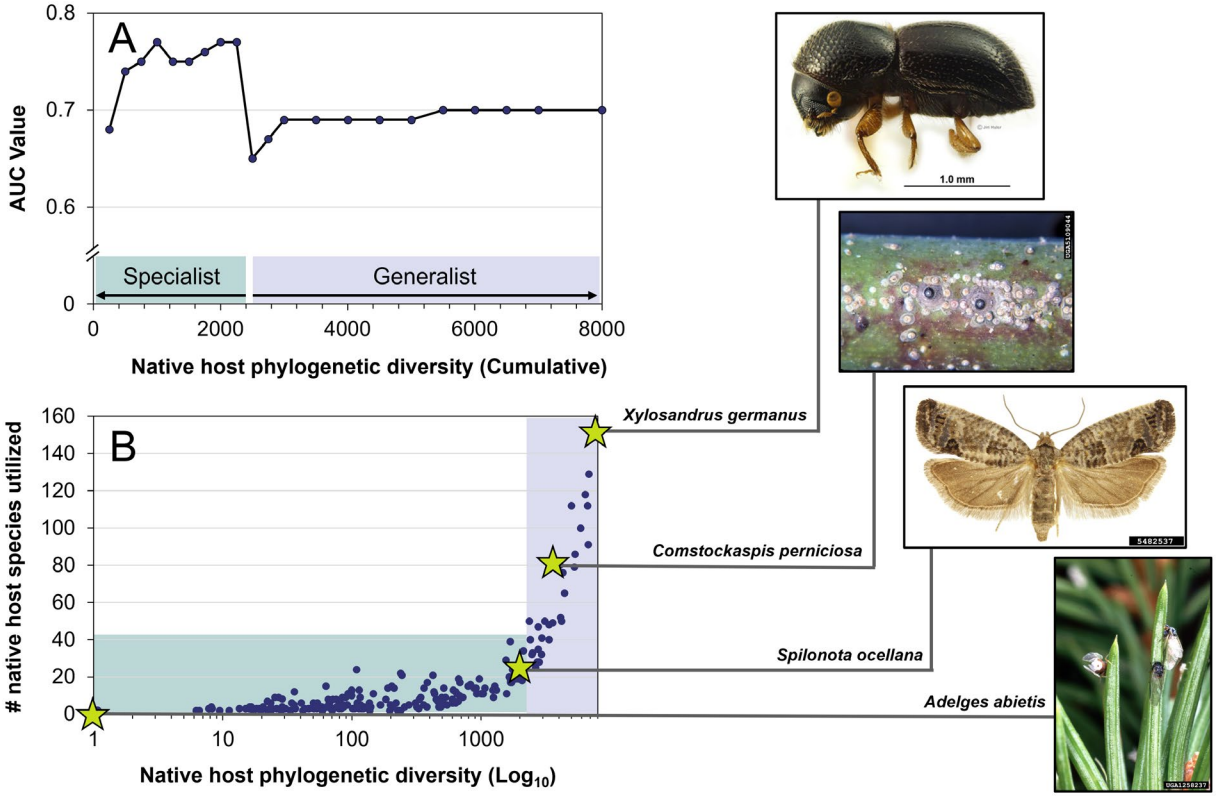

FIGURE 2 | Native host tree phylogenetic diversity calculations. Insects with a phylogenetic diversity < 2250 CMy (specialist, teal colour in A & B) were considered to have a similar host breadth and analysed together, and insects with a phylogenetic diversity ≥ 2250 CMy (generalist, purple colour in A & B) were analysed separately to maximise model predictive ability and strength using area under the curve (AUC) (A). Native host tree phylogenetic diversity highly corresponded with the number of tree species that each insect utilises in its native range (B). Green stars correspond with the insect species pictured, which represent the full range of phylogenetic diversity (0–7723 CMy) represented in our study. Photos (top to bottom) courtesy of J. Hulcr, University of Florida, United States National Collection of Scale Insects Photographs, U.S. Department of Agriculture (USDA) Agricultural Research Service, Bugwood.org, Todd M. Gilligan and Marc E. Epstein, TortAI: Tortricids of Agricultural Importance, USDA APHIS PPQ, Bugwood.org, and Stanislaw Kinelski, Bugwood.org.

challenge with using the traditional binary definition of 'specialist' and 'generalist' or even a more continuous variable like host species richness, is where to draw the line between categories for predictive purposes (Ali and Agrawal 2012). Our results demonstrated a phylogenetic diversity boundary at 2250 CMy for our model of non-native herbivore impact, where insects with host breadth less versus greater than the boundary can be functionally categorised as specialists versus generalists (Figure 2A). This quantitatively defined boundary resulted in some non-native insects that fell within the intermediate area of the continuum (Figure 2B) to shift from a generalist categorization to being in the specialist group. Under traditional categories, some of the insects in this intermediate area might be considered oligophagous. Though conventional definitions would limit them to utilising only one or two families, many in this region of phylogenetic diversity utilise more families of plants.

Non-native insects are thought to be associated with a broader host range than insect pests native to North America, which may help facilitate establishment (Wang et al. 2022). Utilising phylogenetic diversity to delineate this characterisation for non-native species allowed us to evaluate the relationship between native and North American host utilisation beyond the use of species richness. Specifically, we can answer the question, 'Do non-native insects change their host breadth in invaded regions?' The host plants of most non-native insect species had a phylogenetic diversity lower or similar in North America compared to their native range (Figure 3A), with 67% of insects shifting from being a generalist in their native range to a specialist in North America. Of the insects that increased their host diversity, most utilised only a single native species but impacted additional species in the same family in the invaded region.

We also noted differences in insects that were from Asia versus Europe or throughout the Palearctic (Figure 3B). Insects from Asia had a much larger decrease in host breadth (from 1726.7 to 850.2 CMy) than European insect species (from 407.1 to 311.6 CMy), likely due to the higher plant diversity in Asia than Europe (Huntley 1993). The decrease in host breadth from Asia to North America could be attributed, in part, to North America being less floristically diverse than Asia (Qian 2002). However, we also saw a decrease in host breadth from Europe to North America, though North America is more diverse than Europe (Huntley 1993). Further differences were observed between feeding guilds, where gall makers, sap feeders and wood borers had a much narrower host breadth in North America compared to their native range, while folivores, reproductive feeders and root feeders did not have a significant difference in native range and North American host breadth (Figure 3C). Differences in native host range versus North America may be attributed to

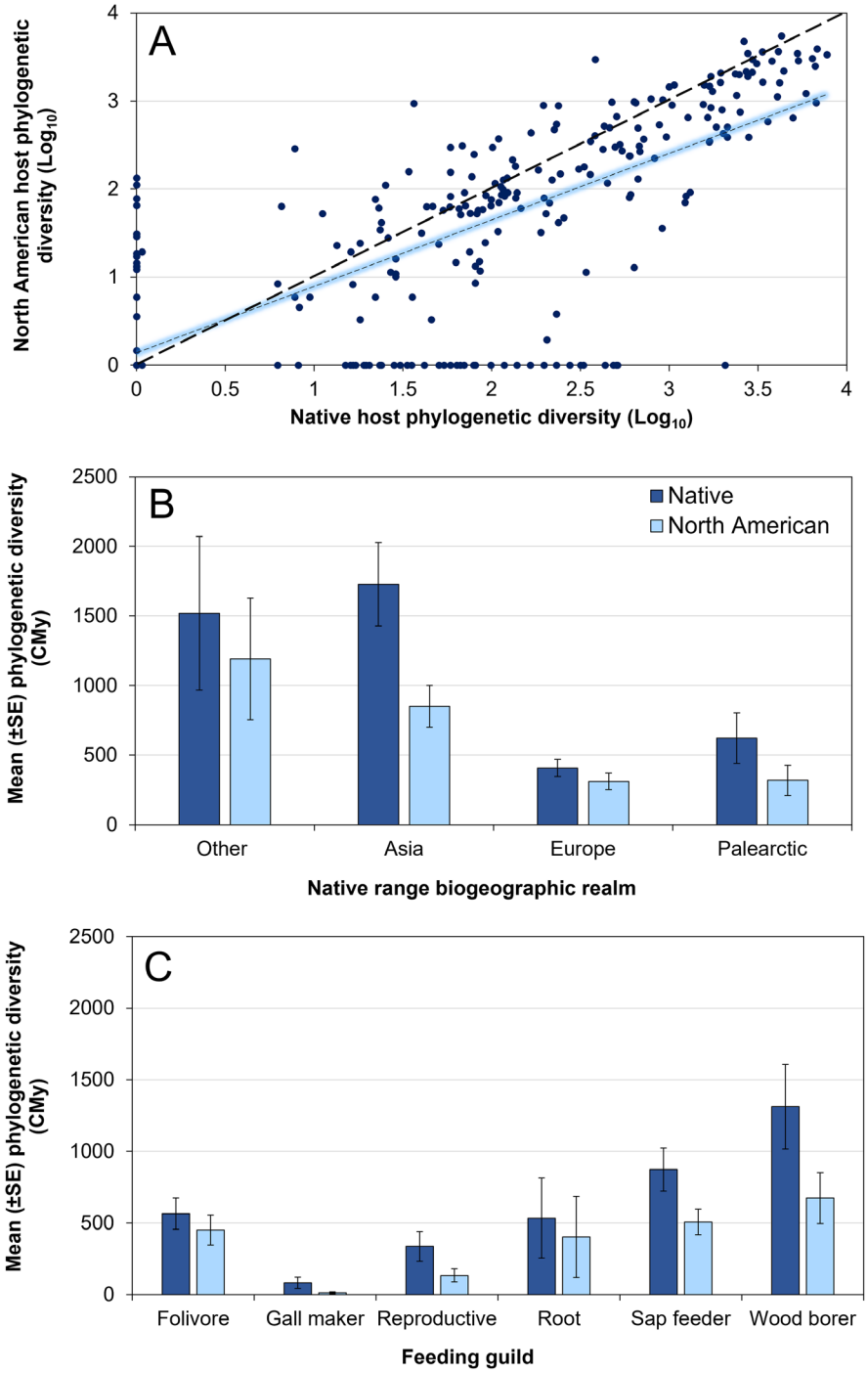

FIGURE 3 | Native host phylogenetic diversity (CMy) was positively correlated with North American host phylogenetic diversity (CMy), with most insect species remaining the same or reducing their host breadth in the invaded region. The observed trend is demonstrated by the blue line, and 1:1 relationship is demonstrated by the thick dashed line (A). Mean (±SE) insect host phylogenetic diversity varied based on (B) the native range biogeographic realm (Asia, Europe, the broader Palearctic or other [Afrotropic, Australasia, Indomalaya, Nearctic, Neotropic]) and (C) insect feeding guild.

the specialised adaptations required of some feeding guilds to overcome the defences of their hosts (Raffa et al. 2016; Thiel et al. 2020).

Quantification of phylogenetic diversity also allowed us to optimise models that allow for the prediction of non-native insect impact, which has remained elusive for over a century. Research on biological invasions has provided insight into rapid ecological and evolutionary shifts. However, the assumptions underlying empirical and theoretical approaches to predicting impact of invasive species have remained largely untested (Raffa et al. 2023). As such, it is imperative to understand the factors that drive non-native species success, and hence, the severe economic and ecological costs they can exert (Lovett et al. 2016; Zenni et al. 2021). Through our effort to predict non-native insect impacts, we found that insect traits, tree traits and tree relatedness had varying significance within each of the three host breadth category models that we developed (Figure 1).

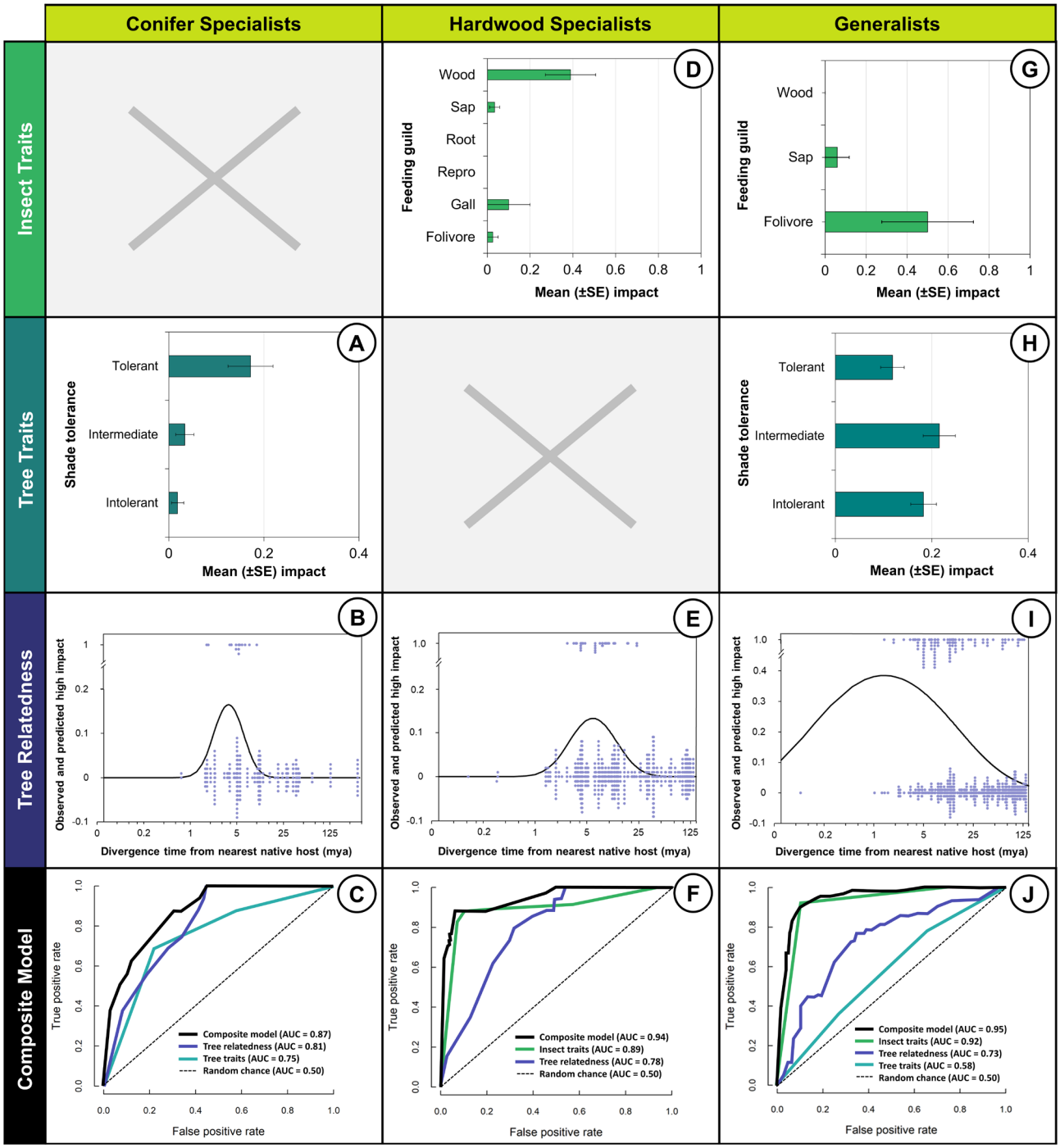

FIGURE 4 | Lettered panels include significant models (top three rows) and composite models (bottom row) that correspond with Figure 1. Panels (D) and (G) show the mean (±SE) impact, ranging from 0 (not high impact) to 1 (high impact), for each insect feeding guild category. Panels (A) and (H) show the mean (±SE) impact of the non-native insects based on the shade tolerance of the North American host trees. In panels (B), (E), and (I), the points represent observed impact, and the lines represent predicted impact. In panels (C), (F), and (J), the colours of the different models vary from the composite model, where the insect traits are in green, the tree (host) traits are in teal, the host phylogeny (tree relatedness) is in purple, and the composite model is in black. Panels with an X indicate the corresponding model was not statistically significant for that host breadth group.

Historically, insect traits have been a major focus for modelling biological invasions (e.g., Fahrner and Aukema 2018) and development of phytosanitary regulations. The only insect trait that predicted impact was feeding guild, with most of the high-impact hardwood specialists being wood borers (e.g., emerald ash borer) and high-impact generalists being folivores (e.g., spongy moth) (Figure 4D,G). These differences in guild may be explained by the impact of host defences on limiting host breadth. Bark and other wood boring beetles must overcome lethal constitutive and induced tree defences as they enter through the bark of the tree, and larvae must survive for long periods of time within the cambial layer of the tree with no avenue of escape (Raffa et al. 2016). These tree defences are substantially reduced by environmental stresses; however, so a key adaptation of bark and wood boring

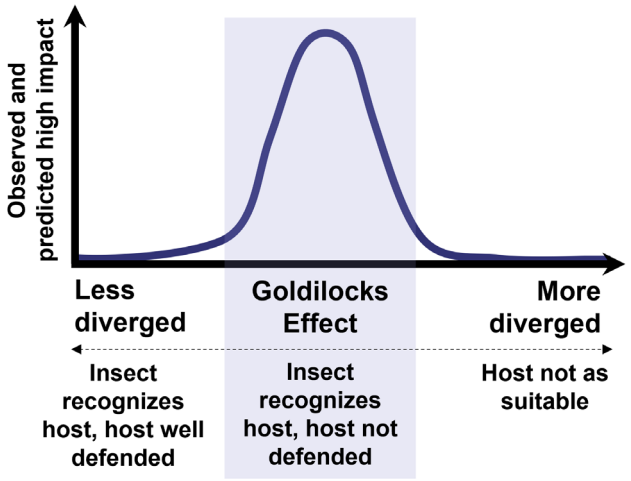

FIGURE 5 | Illustration of the importance of tree relatedness (host evolutionary history) and the 'Goldilocks' effect for evaluating potential impact of a non-native insect on a novel host. This figure corresponds with Figure 4B,E,I.

insects is their ability to locate and select poorly defended individuals within the host species population. Conversely, folivores adapt to plant chemistry and trichomes (Volf et al. 2015), or can avoid host defences by moving off the foliage (Thiel et al. 2020). Though sap feeders comprise a substantial portion of non-native insects, they pose less of a risk than wood boring insects and folivores. This result may be surprising given the high impact of hemlock woolly adelgid and balsam woolly adelgid (*Adelges piceae* Ratzeburg), but it reflects the pattern that trees are commonly tolerant of the direct effects of sap feeding except where hypersensitive reactions or vectored pathogens are involved (Koch et al. 2016).

Interestingly, shade-tolerant trees were most susceptible to non-native conifer specialists, but the least at-risk from non-native generalists (Figure 4A,H). Although shade tolerance is typically associated with effective defences (Kitajima 1994), some non-native specialists may have adaptations to overcome defences on trees that may have a limited ability to tolerate herbivory due to low carbon assimilation in light-limited environments (Coley et al. 1985; Strauss and Agrawal 1999). Conversely, non-native generalists may not be able to tolerate defences as well as specialised insect species, making them less impactful on shade-tolerant species (Agrawal and Sherriffs 2001).

Tree relatedness was the only model that was significant for all three host breadth categories (Figures 1 and 4; Tables S9 and S10). For each quadratic model, we identified a 'Goldilocks' zone of host relatedness, such that the highest risk of high impact was for non-native insects with a native host that is neither too recently nor too distantly diverged from the North American host (Figure 5). Tree species too closely related may retain previously evolved defences or tolerance to novel herbivores, whereas plants too distantly related may have diverged too long to be suitable hosts (Mattson et al. 1988; Gandhi and Herms 2010; Gilbert et al. 2015). Peak probability of high impact occurred at different divergence times for the three host breadth categories, which may be attributed to differences in the most impactful feeding guilds for each host breadth category, and their adaptations and responses to defences. Though the tree relatedness models had great predictive ability, the merged composite model had the greatest predictive ability for all three host breadth categories (Figure 4C,F,J; Table S11), suggesting that there are multiple factors that must be considered when forecasting non-native insect impact.

We acknowledge some limitations to these models. For example, host records may be missing for some insects due to unequal historical research focus. Some records may be uncertain because an observation of an insect's presence on a plant does not mean that the insect can utilise the plant for survival and reproduction (Cunningham and Zalucki 2014). Some factors, such as native range climate, are not included in these models, as they may be more important for predicting insect establishment success (Yamanaka et al. 2024) than impact. We are confident that we provided a robust sample of non-native insect traits and hosts for our model to effectively estimate impact. As more insects arrive and impact trees, there will undoubtedly be opportunities to amend the dataset and evaluate more finely honed ways to subdivide the model. These models can be expanded to incorporate indirect, chronic and sector-specific impacts not included in our analyses.

Our results demonstrate how phylogenetically based host breadth can be used to develop models that apply attributes of non-native species to estimate their potential impacts. This is extremely valuable for risk assessments that can inform policy and management (Leung et al. 2012; Lodge et al. 2016). Herbivore host range occurs on a continuum from a narrow set of phytochemically- and phylogenetically-related hosts (specialists) to a wide variety of evolutionarily divergent hosts (generalists) (Fordyce et al. 2016). By quantifying and functionally characterising host breadth, we can more confidently predict future impacts of non-native insects, including those that have already been introduced but have not yet realised their impacts (Mech et al. 2019; Schulz et al. 2021) or could be on their way (Uden et al. 2023). This approach could also be used to develop models that predict impact for forest pests that invade other regions (e.g., North American insects in Europe or Asia), evaluate the drivers of phytophagous insect impact on herbaceous plants, or assess impacts of non-native vertebrate herbivores on their hosts. In all cases, predictive models could help forecast impacts on host plants, which could improve biosecurity, increase efficiency of regulatory protocols and reduce control costs (Tobin et al. 2014).

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Acknowledgements

We thank Ian Pearse for reviewing a draft of this manuscript, David Campbell (University of Washington) and Terry Arundel (U.S. Geological Survey, USGS) for database assistance, Brittany Barnes

(University of Georgia), Karla Boyd (University of Maine), Lekeah Durden (USGS-NFS Graduate Research Intern), Chithra Singareddy (Dartmouth College), Erika Teach (The Davey Tree Expert Company) and Atticus Wolf (USGS) for assistance with data entry, Jessen Havill (Bucknell University) for helping to write programming scripts, and Tom Edwards (USGS) who led a workshop on species distribution modelling in R that informed development of portions of the analysis.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All insect, host plant, affiliated trait and reference data for the insects included in this study are documented in U.S. Geological Survey ScienceBase (Schulz, Mech, Havill, Hoover, et al. 2024; https://doi.org/10.5066/P9XT5LNP). Code and input data sets for analyses included in this study are available in Zenodo (Schulz, Mech, Havill, Uden, et al. 2024; https://doi.org/10.5281/zenodo.14562802).

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70083.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.