The Effect of Evolutionary History on Plant-Insect and Plant-Pathogen Interactions

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Abstract

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It is impossible to overstate the importance of plants to life on this planet, and in terms of global carbon flux and food chains, autotrophic plants are among the most important organisms on Earth. The rise of photosynthetic plant life as a dominant force on earth altered the atmosphere into the oxygen rich air we breathe and sustains the food web we require to survive. This rise in available oxygen happened slowly at first, with cyanobacteria gradually releasing their waste as oxygen into the early oceans, and suddenly rose with a dramatic increase in atmospheric oxygen during the Great Oxidation Event. While this event was a death sentence for the large population of anaerobic organisms living at the time, it has allowed the enormous families of oxygen-dependent forms of life that we know today. Among all multicellular organisms, only plants have the ability to convert sunlight into organic substances via photosynthesis and are therefore able to live a more or less independent life, and their presence has shaped the ecosystems around them ever since. Humans have depended on plants since prehistory to satisfy their basic needs such as food, clothing, shelter, and medicine. One of the most serious and urgent threats to both

agricultural and ecological plant systems are invasive species, especially invasive insect herbivores and plant pathogens that pose threats to plant health globally, resulting in significant ecological and economic damage.

Prior to the age of human exploration, dispersal of species from one area to another was constrained by geographical, climatological, and biological barriers. For example, species were generally unable to cross oceans or mountains, could not survive a journey across a desert, or simply lacked the ability to move long distances. Consequently, the movement of species into new areas was limited to rare, stochastic dispersal events (i.e., such as those that were atmospherically-mediated), or relatively slow events such as continental drift or temporary land bridges due to global climate changes. While the ebb and flow of species is a natural process, the anthropogenic movement of species has accelerated their introduction into novel habitats.

It is widely recognized that most non-native insect, pathogen, and weed species arrive in their new locations as a result of global trade and travel, and species may be transported inadvertently with their hosts when nursery stock, produce, or related commodities are shipped. Humans have transported and traded plant and animal species for millennia, with notable jumps in volume following European global expansion beginning in the 1500s, the industrial revolution, and in recent decades during the age of modern transportation mechanisms. With current trends in global trade, invasive species have caused, and will continue to cause, enormous ecological and economic damage, and understanding and managing invasive species are critical for protecting and restoring resilient ecosystems. Invasive species of all types can pose considerable harm to ecosystems, ecological processes, and both local and national economies, and can substantially alter the composition, structure, or function of native terrestrial and aquatic systems. Fortunately, only a minority of the species that arrive in a new environment are thought to successfully

establish, and only a minority of them rise to the level of a high impact invasive species. Indeed, studies have found that about 10 percent of invasive species survive transport and introduction, about 10 percent of those that survive are able to establish to self-sustaining levels, and only about 10 percent of those cause significant ecological or economic damage (Williamson & Fitter 1996). This small minority of invaders, however, cause high impacts exceeding US$70 billion annually just in North America, which makes it imperative to predict which species pose the greatest risk

The ability to implement eradication strategies against invasive species tends to be feasible only over a relatively short window. Before and just after a successful introduction, prevention and eradication are relatively low cost and have a higher probability of success. However, as invasive species become established over a larger area, the cost rapidly increases and the effectiveness of remedial measures rapidly decreases, making control economically infeasible or realistically impossible. It is therefore critical to identify and implement control measures early. Regulatory measures focused on prevention and early detection of alien pests include the listing of quarantine pests and plant passports/quarantine inspections, but such interventions can be hampered by a lack of knowledge on potential pests and novel pest-host interactions. Moreover, because many invasive insects and pathogens pose little harm in their native habitat, and thus are often unknown to managers, there tends to be critical knowledge gaps when they are introduced into a novel environment.

Plants are also not passive organisms that merely sequester CO2 from the atmosphere until they are eaten, and nature is full of examples of plants influencing their environment, herbivores, pollinators, and other co-habitants. Co-evolution between herbivores and their plant hosts, as well as pressures from competition, predation, and parasitism, contribute to the complexity and

stability of natural ecosystems. Two hypotheses in invasion biology consider the role of coevolutionary relationships in non-native species establishment and impact. One, the enemy release hypothesis, states that introduced species establish and spread because they are liberated from their co-evolved natural enemies. This hypothesis is supported with empirical support in the success of classical biological control strategies. The second, the defense free space hypothesis, states that a lack of adequate defenses in evolutionarily naïve hosts creates opportunities for non-native species to establish due to their lack of coevolutionary history with the invader. Lack of coevolved defenses against some invasive herbivorous insects has been documented, but relatively few studies have focused on this relationship. Only recently have quantitative studies looked at if and how these evolutionary relationships affect species invasiveness, with evidence suggesting that the divergence time between native and novel plant hosts is predictive of herbivorous insect impact.

Studies that attempt to address the potential role of evolutionary history on interactions between plants and non-native herbivores and plant pathogens could benefit from the use of the plant collections within botanical gardens. Indeed, botanical gardens are recognized for their value in biosecurity research, such as the use of sentinel host plants to identify insect and pathogen incursions. Botanical gardens contain a diverse collection of native and non-native plant species, and are often located in urban areas, which places them in close proximity to high-risk introduction sites including sea ports, airports, and human dwellings. Arboreta and botanic gardens amass collections of plants from all over the world and, unintentionally, insects and plant diseases from other regions, which presents the serendipitous opportunity to identify and document new associations between plants and the pests and diseases that attack them. Botanic gardens have an institutional capacity to contribute to scientific studies of these pests and

diseases, stemming from the living and preserved collections of plant diversity they develop and curate, coupled with their expertise in plant taxonomy, identification, propagation, and cultivation.

Due to the plant resources available at the University of Washington Botanic Gardens, I used some of its plant collection for field experiments in support of my PhD dissertation research. During the time I conducted my field research, the Washington Park Arboretum was managed cooperatively by Seattle Parks and Recreation and the University of Washington. Within the physical space of the Washington Park Arboretum, the plant collections are a critical element of the educational, research, and outreach mission of the University of Washington. The property that constitutes the present Washington Park Arboretum includes two north-south ridges and the valley between, and is characterized by the natural drainage of small streams running north into wetlands and to Union Bay. The plant collections include over 14,500 accessioned specimens in the collections; over 4,000 different types of trees, shrubs and other plants native to 98 countries, which serve as vital resources for scientific study.

For my doctoral research, I conducted three studies, each approaching the protection of plant collections from invasive species from a different perspective. In the first chapter, I conducted a field and laboratory-based study to measure the relationship between an introduced insect herbivore, the mountain ash sawfly (*Pristiphora geniculata* (Hartig)) and host species within *Sorbus* from around the world. In this chapter, I tested the hypothesis that host species from the native range of *P. geniculata*, presumed to be Europe, would have more effective co-evolved defenses against this folivore, resulting in reduced larval feeding performance and fitness as proxied by pupal weight, relative to evolutionarily-naive host species, such as those native to Asia and North America. In the second chapter, I used data collected on an introduced insect

herbivore, the cherry bark tortrix (*Enarmonia formosana* (Scopoli) (Lepidoptera: Tortricidae), and a fungal pathogen that causes cherry brown rot (*Monilinia fructicola* Wint. and *Monilinia laxa* Aderhold & Ruhland) over a 10-year period. This dataset was used to evaluate the response of *Prunus* spp. from different subgenera and different native regions, as well as various climactic conditions, to cherry bark tortrix and *Monilinia* spp. In the third chapter, I conducted a literature review to predict, using published models, which insect species native to Asia but not yet established in North America are most likely to threaten woody plants native to the Pacific Northwest. Each of these studies will advance our understanding of the role of evolutionary history on plant-insect and plant-pathogen interactions.

Table of Contents

List of Figures

List of Tables

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Chapter 1 The role of host phylogenetic history on *Pristiphora geniculata* (Hartig) larval performance

Abstract

The genus *Sorbus* L. sensu lato (s.l.) comprises more than 250 species of trees and shrubs in the family Rosaceae, including both simple-leaved and pinnately compound-leaved taxa. Its native distribution spans the temperate zone of the Northern Hemisphere. Many species are widely cultivated as ornamentals, valued for their showy red, yellow, or white fruits and their often striking autumn foliage. The mountain-ash sawfly, *Pristiphora geniculata* (Hartig) (Hymenoptera: Tenthredinidae), is a folivorous insect associated with *Sorbus* spp. It is native to Europe but has been introduced into both Asia and North America. Its spread provides a useful system for examining how host novelty and evolutionary history influence herbivore performance in novel environments.

Two major hypotheses in invasion biology address the role of evolutionary history in the establishment and impact of non-native species. The enemy release hypothesis proposes that introduced species succeed because they are freed from their co-evolved natural enemies. In contrast, the defense free space hypothesis predicts that evolutionarily naïve hosts may lack effective defenses against novel herbivores due to limited coevolutionary history, creating opportunities for increased herbivore success. This hypothesis was tested using the *Sorbus* collection at the Washington Park Arboretum. I hypothesized that evolutionarily naïve *Sorbus* species would be less defended against feeding by *P. geniculata* larvae, resulting in higher herbivore performance. I further predicted that herbivore response would vary across the

evolutionary history of *Sorbus*, with European and Eurasian species being more resistant than Asian and North American taxa.

This study provides a mechanistic test of models which seek to identify factors associated with the invasiveness and performance of insect herbivores. Using cocoon weight as a proxy for fitness, I quantified *P. geniculata* performance across host plants, comparing larvae feeding on its native host (*S. aucuparia* from Europe) with those feeding on *Sorbus* taxa from Asia, Eurasia, and North America. The Washington Park Arboretum *Sorbus* collection provides a particularly suitable system for this comparison, as it includes broad phylogenetic and biogeographic representation of the genus. Notably, *P. geniculata* is a relatively recent introduction in Washington, and there is a scarcity of ecological information from both its invaded and native ranges, with only limited historical studies available. I observed that host plant taxonomy strongly influenced larval developmental performance in *P. geniculata*, with effects structured across both species-level and subgeneric boundaries within *Sorbus*. These findings support the hypothesis that host-associated herbivore performance is, at least in part, shaped by the evolutionary relationships among host taxa.

Introduction

The genus *Sorbus* L. *sensu lato* (s.l.) comprises over 250 trees and shrubs in the family Rosaceae, characterized by both simple-leaved species and pinnately compound-leaved species. Its native range includes the temperate zone of the Northern Hemisphere (McAllister 2010). Rosaceae is a moderately large angiosperm lineage, with approximately 3000 species in 100 genera, including a clade of mostly fleshy-fruited genera, some of which are widely cultivated and of considerable economic importance (e.g., apple (*Malus*), chokeberry (*Aronia*), loquat (*Eriobotrya*), pear (*Pyrus*), quince (*Cydonia*), and serviceberry (*Amelanchier*)) (Lo and Donoghue 2012). Apple and many of its relatives, including *Sorbu*s, have a distinctive fruit, a pome, which led to the identification of these plants as a group by Bauhin in 1623; this group of pome-bearing plants has long been known within the subfamily Maloideae (Kovanda 1965, Campbell et al. 2007). The placement of *Sorbus* within Maloideae, and its relationship to its near relatives, has been a point of considerable debate, and the generic limits have been quite fluid in Maloideae (Robertson et al. 1991). This difficulty in classification can be attributed to the presence of apomixis within *Sorbus*, which is also present in its close relatives *Cotoneaster*, *Crataegus*, *Amelanchier*, *Aria*, and *Malus* (McAllister 2010). Apomixis is a form of asexual reproduction involving production of fruit and seed without fertilization, resulting in seedlings that are genetically identical to the parent plant (McAllister 2010). In general, apomixis in Sorbus is associated with the doubling or multiplication of chromosomes following intergeneric hybridization (triploids and tetraploids) although diploid apomicts of *Sorbus* are also known (McAllister 2010, Hamston et al. 2018). Many hybrids are sterile; however, occasionally intergeneric hybrids within *Sorbus* will inherit apomixis, allowing one plant to reliably reproduce from seed and start a self-sustaining population (McAllister 2010). The discovery of

hybridization and apomixis in *Sorbus* is relatively recent (Gillham & McAllister 1977), and combined with a lack of genomic analysis, helps explain the historical confusion in its taxonomic classification (McAllister 2010).

For example, before recent taxonomic revisions, whitebeam (as *S. aria*, etc.), service tree (as *S. domestica*), and wild service tree (as *S. torminalis*) were included within the genus *Sorbus*. However, recent molecular and morphological evidence suggests that *Sorbus* sensu lato contains several polyphyletic genera (Campbell et al. 2007, Lo and Donoghue 2012, Potter et al. 2007). Recent treatments classify former *Sorbus* subgenus *Sorbus* (commonly known as rowan or mountain ash) as *Sorbus* s.s., and raise the other subgenera to generic rank as *Aria*, *Chamaemespilus*, *Cormus* and *Torminalis* (Robertson et al. 1991, McAllister 2005, Campbell et al 2007, Potter et al. 2007, Ulaszewski et al. 2021). Any further reference to *Sorbus* is *sensu stricto* unless noted.

Ancestral range reconstructions showed high support for an origin of *Sorbus* in the middle Eocene in eastern Asia and a complex subsequent biogeographic history that resulted from dispersal and vicariance events in different time periods and directions (Li et al. 2017). Four dispersal events are assumed to explain the wide distribution of *Sorbus* in the temperate zone and diversification in the edges of the Tibetan Plateau (Li et al. 2017). The first occurred around southwest China and adjacent areas, followed by a dispersal event to the Tianshan Mountain ranges around 30 mya (Li et al. 2017). Further migration to North America occurred at two different times (around 26 and 16 mya), and another dispersal event occurred through Siberia to Europe around 9 mya (Li et al. 2017). These dispersal events resulted in two major lineages within *Sorbus* that are supported by phylogenetic analysis (Li et al. 2017) and coincide with two previously defined subgenera, *Sorbus* and *Albo-carmesinae* (McAllister 2005).

The *Albo-carmesinae* lineage comprises three well supported clades: Tianshanicae, Multijugae, and Discolores. The Tianshanicae clade diverged during the Oligocene, when some *Sorbus* from the ancestral range dispersed to the Tianshan Mountain ranges (Li et al. 2017). This population was then isolated by the northern Tibetan Plateau uplift, which occurred when the Indian continental plate shifted northward and was subducted beneath the Eurasian plate, causing intense tectonic movements and the uplift of the Tibetan Plateau (Liu et al. 2015). At that time, the southwest Asian monsoon penetrated into the Tianshan mountains, providing ideal conditions for *Sorbus* to not only colonize that area, but to thrive and diversify (Li et al. 2017). However, further uplift cut off this area from the monsoon, decreasing precipitation and isolating the Tianshanicae clade. The Discolores-Multijugae clade, which comprises ~40 species distributed around the edge of the Tibetan Plateau and part of eastern China Mountains, was strongly supported as emerging from southwest China and adjacent areas in the early Miocene (Li et al. 2017).

The core *Sorbus* lineage includes two well-supported clades, Aucupariae and Commixtae, distributed from the south and east border of the Tibetan Plateau to the mountains of central China, north China, and Japan, extending as far as North America and Europe (Li et al. 2017). Global climatic shifts were an important part of this long-distance dispersal. The common ancestor of the Aucupariae and Commixtae clades existed in eastern Asia in the late Eocene, and was likely to prefer cool habitats as most *Sorbus* species do today (Li et al. 2017). Around the time that *Sorbus* originated, a cooling event happened (Middle Eocene), followed by a slight warming in the late Eocene, and later a more extreme cooling in the earliest Oligocene (Prothero 1994). During the early middle Miocene, global temperatures cooled, causing the warm-temperate environments to evacuate from Northern Asia and Europe (Zachos et al. 2001), which

likely opened up opportunities for dispersal of *Sorbus* from Siberia to Europe. Meanwhile, *Sorbus* species from both Aucupariae and Commixtae clades dispersed eastward from Asia, reaching North America twice, at different times (26 and 16 mya). The red-colored fruits found in the core *Sorbus* lineages are attractive to birds, suggesting that birds have played an important role in helping these lineages to move to new biomes and ecological habitats; indeed, blackbirds, song thrushes, and American robins (all members of *Turdus*, a genus with cosmopolitan distribution) are the main dispersers of *Sorbus* fruit (Klicka et al. 2005, Li et al. 2017). The formation of a land bridge between Siberia and Alaska during periods of sharp drops in global temperatures in the Miocene is known to be important for the movement of *Sorbus* species (Hopkins 1959). This land bridge, in combination with seed dispersal by birds, could explain the extensive geographic distribution of the core *Sorbus* clades.

The mountain-ash sawfly, *Pristiphora geniculata* (Hartig) (Hymenoptera: Tenthredinidae), is a folivore of *Sorbus* spp. It is native to Europe but has been introduced in Asia and North America. There are only a few published historical records on its distribution in Europe where it was first described in 1840 by Theodor Hartig. It was first detected in the United States in New York and Massachusetts in 1926 (Schaffner 1936). It subsequently spread throughout the northeastern US states and Canadian provinces, and west to Minnesota and Ontario (Krombein et al. 1979). The species was first detected in Washington State in 2009, and is now distributed throughout the Puget Sound region (Looney et al. 2016). The larvae are voracious feeders and can almost completely defoliate healthy trees; however, mortality of even repeatedly defoliated trees is infrequent (Forbes and Daviault 1964). There are no records of *P. geniculata* being collected in Europe from any host but European mountain ash, *Sorbus aucuparia* L. (Forbes & Daviault 1964). In Eastern Canada, it has been collected from *S. aucuparia*, and American mountain ash,

Sorbus americana Marshall, showy mountain ash, *Sorbus decora* (Sargent) Schneider, and on *Sorbaronia hybrida* (Moench) Schneider (Forbes & Daviault 1964). In the Washington Park Arboretum, Seattle, WA, it has been found feeding on *Sorbus scopulina* Greene, *Sorbus microphylla* Wenz., *Sorbus* 'Birgitta', as well as the aforementioned *S. aucuparia*, *S. americana*, and *S. decora* (Garrison, unpublished data). There are no records of *P. geniculata* feeding on plant hosts of *Sorbus* s.l. (Aria spp., etc.) outside of *Sorbus* s.s. The *Sorbus* collection at the Washington Park Arboretum presents an excellent system to study the relationship between *P. geniculata* and its potential hosts, having representatives of every clade and biogeographic region from which *Sorbus* grows. Additionally, because *P. geniculata* is a relatively recently introduced species in Washington, prior studies examining its behavior in the Pacific Northwest are nonexistent. In fact, there appears to be no studies of this insect in its native range, only one from Northeast Canada (Forbes & Daviault 1964), and apparently no studies that have reported on its potential host range.

Prior descriptions and keys to *Pristiphora* spp. are available in Konow (1902), Enslin (1912-1917), Morice (1922), Lorenz and Kraus (1957), and Benson (1958). Forbes and Daviault (1964) provide a description of the life cycle of *P. geniculata*. Briefly, two generations per year are reported in Europe and eastern Canada, one in northern Quebec, and two have been observed in Western Washington (Garrison, unpublished data). The second generation is smaller in abundance than the first, and usually only minor defoliation occurs during the second generation. The sawfly overwinters as a larva in a cocoon in the ground or in debris beneath infested trees. Pupation occurs in the spring and adults emerge from late May to early July. Eggs are usually laid within one or two days of adult emergence, and hatch in six or seven days at a mean daily temperature of 21°C (Forbes & Daviault 1964). Male larvae have four instars and feed for about

two weeks, and female larvae have five instars and feed for about three weeks. The larvae drop or crawl to the ground and spin cocoons in the litter or soil. In Western Washington, adults emerge from ~20% of these and give rise to a second generation, which hatches in late July, feeds, and drops to the soil by mid-August (Garrison, unpublished data).

Two well established hypotheses in invasion biology address the importance of evolutionary history in non-native species establishment and impact. The first of these, the enemy release hypothesis, states that introduced species establish and spread because they are liberated from their co-evolved natural enemies (Liu & Stiling 2006, Meijer et al. 2016). This hypothesis is well supported with empirical support in the success of classical biological control strategies (Caltagirone 2003, Elkinton et al. 2006). In fact, a host-specific and solitary endoparasitoid, *Olesicampe geniculatae* Quednau and Lim, was successfully established in Quebec following introductions from its native Europe and has been associated with reduced populations of *P. geniculata* (West et al. 1994). However, to date, this parasitoid has not been observed in the Pacific Northwest.

The second hypothesis, the defense free space hypothesis, states that a lack of adequate defenses in evolutionarily naïve hosts creates opportunities for non-native species due to their lack of coevolutionary history with the invader (Desurmont et al. 2011, Gandhi & Herms 2010). This hypothesis was tested using the *Sorbus* collection at the Washington Park Arboretum. I hypothesize that evolutionarily naïve *Sorbus* species are less defended against feeding by *P. geniculata* larvae, resulting in increased insect herbivore performance. I also hypothesized that the herbivore response will vary across the evolutionary history of *Sorbus*, such that European and Eurasian *Sorbus* species will be better defended than Asian or North American species. This proposed study provides a mechanistic test of the models proposed by Mech et al. (2019) and

Schulz et al. (2021), which aimed to quantify factors associated with invasiveness in insect herbivores. Using cocoon weight as a proxy for fitness, I quantified and compared *P. geniculata* fitness while feeding on its native host (*S. aucuparia* from Europe), to those feeding on *Sorbus* from outside its native range (e.g. *Sorbus* from North America, Eurasia and Asia).

Materials and Methods

Study Area

The study site for this experiment was the Washington Park Arboretum in Seattle, WA, USA. The *Sorbus* collection at the Arboretum is one of the earliest collections established in the Arboretum, and was initiated shortly after World War II under the directorship of Brian Mulligan (BOLA 2003). In 1990, the collection was renovated and named the Brian O. Mulligan *Sorbus* Collection. It is located between the western border of the Washington Park Arboretum and Arboretum Drive East. The *Sorbus* collection is still organized taxonomically as *Sorbus sensu lato*, with compound leaf forms (*Sorbus* s.s.) concentrated at the south end of the collection, and simple leaf forms (*Aria* spp., *Torminalis* sp., and intergeneric hybrids) planted at the north end. The *Sorbus* (s.s.) collection currently contains 69 plants representing 38 different species and/or cultivars.

Preliminary rearing studies

In early June of 2021, defoliation was observed on several *Sorbus* plants in the Washington Park Arboretum (Fig, 1), and *P. geniculata* larvae were found feeding (Figure 2). Beginning in July, larvae of *P. geniculata* were collected in 3.8-liter glass jars with 2.54 cm of sandy soil added (Fig 3). New *Sorbus* foliage was added as the larvae consumed available foliage in the jar. These

larvae were successfully reared to the pupal stage, and pupae subsequently emerged as adults, providing proof of concept for further experimentation involving laboratory rearing.

Data collection (2022, 2023, and 2024)

In early 2022, the *Sorbus* collection at the Washington Park Arboretum was evaluated for suitability for inclusion in the study. This included an assessment of overall plant health and size, and determining if removing the required amount of foliage for experimentation would be detrimental to plant health. Of the 38 different species and/or cultivars of available *Sorbus*, 13 species were initially selected across the phylogeny and biogeography of *Sorbus* (Figure 4). The subgenus of each species was determined from previous studies on *Sorbus* phylogeny (Li et al. 2017, Tang et al. 2022). However, *S. randaiensis* was not represented in any of these studies so a Maximum Likelihood phylogenetic analysis was performed using MEGA 12 software (Kumar et al. 2024) using complete chloroplast data downloaded from the National Center for Biotechnology Information (NCBI) dataset (O' Leary et al. 2024). This analysis showed that *S. randaiensis* is most closely related to *S. sargentiana*, *S. aucuparia*, *S. scopulina*. Thus, for the analysis of subgenera, *S. randaiensis* was placed in the Aucupariae clade (Figure 5).

In early May of 2022, foliage from *S. aucuparia* that presumably contained *P. geniculata* eggs, as noted by the characteristic lesions on the leaf margins, were collected from Snohomish County, WA, and the Washington Park Arboretum. For each of the 13 selected *Sorbus* species, three replicated ~7.6 L buckets were set up. To provide a late instar and pupation site, sandy soil from the Washington Park Arboretum field nursery was passed through a 6.3 mm sieve, and a 25 mm deep layer of soil was placed in each bucket. Infested leaves with ~175 lesions (assumed to be *P. geniculata* eggs) were placed in each bucket with the respective foliage from each *Sorbus* species. The buckets were covered with a fine mesh fabric to prevent escape and allow air flow.

Fresh foliage from each *Sorbus* species was replenished in each bucket approximately every 3-4 days. Foliage was collected from one specimen of each species in the *Sorbus* collection and taken to the Arboretum Apiary where the buckets were set up (Figure 6). This site is behind a split rail fence, providing a location protected from curious members of the public and giving the larvae ambient temperature and weather conditions. Also, in 2022 it was noticed that some foliage dried out before the larvae were able to consume it, and larvae would disperse throughout the bucket searching for food, potentially reducing fitness and skewing data. To prevent leaf desiccation due to transpiration, collected leaflets were inserted into 7.6 cm floral water tubes filled with water (Fig 7). The floral tubes were placed into the soil at an angle so foliage was relatively in a natural horizontal position. When new foliage was added, it would be placed perpendicular to and intersecting the existing foliage to make it easy for larvae to find and travel to fresh foliage. Occasionally larvae would fall to the soil when new foliage was added, and in these cases the larvae would be carefully scooped up with a spoon and placed on new foliage.

Unfortunately, very few larvae were observed following inoculation, suggesting that either the lesions were not *P. geniculata* eggs, despite being similar in appearance to published photographs (Forbes & Daviault 1964), or egg hatch was unsuccessful. Thus, when early instars were observed from the field at the Washington Park Arboretum on five different *Sorbus* species, larvae were collected from each host species, along with the leaves on which they were feeding, and placed into 3.8 L containers with 2.54 cm of soil (as indicated above): *S. americana* (162 larvae), *S. aucuparia* (44 larvae), *S. decora* (223 larvae), *S. gonggashanica* (24 larvae), and *S. randaiensis* (77 larvae). When no larvae were observed on foliage, the buckets were collected and taken to the lab. In the lab, any remaining foliage was inspected for cocoons and the soil in each bucket was put through a 2.0 mm sieve to collect cocoons. Cocoons were subsequently

collected in later summer, gently cleaned, and individually weighed to the thousandth of a gram using an Ohaus PA84 analytical scale. Cocoon length was also measured to the thousandth of a mm using a Traceable brand electronic digital caliper. Cocoons were maintained under ambient conditions (~20 C, 65% RH, 12:12 L:D photoperiod) to allow for second generation adult emergence. After 12 weeks, any remaining cocoons were placed in a covered but open structure at the Washington Park Arboretum to experience ambient winter conditions until the following spring, at which time they were monitored for adult emergence.

This experimental design was repeated in 2023 and 2024. Scouting for eggs and larvae began in early June. Although eggs were not found, early instars were found in Snohomish County and the Washington Park Arboretum on 8 June 2023, and an adult was found on *Sorbus* 'Brigitta' on 15 June 2023 (Fig 8). A total of 526 early instars were collected from *Sorbus* spp. This number was insufficient to inoculate all 13 host species from 2022 at appropriate levels of replication, and to maintain an inoculation density of ~20 *P. geniculata* larvae per bucket. Thus, the same host species from the preliminary rearing studies in 2022 and *S. cashmiriana* were inoculated in 2023. In 2024, *P. geniculata* larvae were found on a specimen of *Sorbus microphylla*, and this species was added in 2024. Across all study years, the host species represented four of the five subgenera and clades in the phylogeny of *Sorbus* (*Commixtae*, *Aucupariae*, *Multijugae*, and *Tianshanicae*) (Figure 4).

Statistical Analyses

Initially, pupal weight and pupal length were considered as response variables since both are a proxy for larval feeding performance, and given that pupal size is positively correlated with fitness (Beukeboom 2018, Enriquez et al. 2022). However, since pupal weight and length were expected to be correlated, I first measured Pearson's product-moment correlation between weight and length in R (R Core Team 2026), which resulted in a significantly positive correlation ($r=0.77$, $p<0.001$). Therefore, I used only pupal weight in subsequent data analysis; pupal weight was chosen instead of length due to increased accuracy during weighing. Pupal weights were transformed using $\log_{10}$ to meet the assumption of normality. I used three models to test the effect of *Sorbus* phylogenetic history on the $\log_{10}$-transformed pupal weights. The first considered the effect of two different *Sorbus* core lineages, *Sorbus* and Albo-caresinae. I also examined the effect of clade (subgenera) and species in subsequent models. Data were used across all years, and year was initially included as a random effect; however, the inclusion of year as a random effect was not successful as variation among years was either negligible or confounded with species variation in the dataset. Data were analyzed in a Generalized Linear Model in R (R Core Team 2026). Post-hoc tests using Tukey's HSD and $\alpha=0.05$ were used for the subgenus and species. Lastly, I calculated the median pupal weight of *P. geniculata* larvae when feeding on its evolutionary-native host species, *S. aucuparia*, as a baseline of larval performance (0.0144 grams). I then divided the weight of each larva when feeding on their other *Sorbus* host species by this median baseline weight to develop a relative growth ratio; for example, ratios >1 would indicate greater larval performance relative to the native host, and ratios <1 would indicate reduced larval performance relative to the native host.

Results

The number of larvae used to inoculate each species and the number of intact pupae recovered per year is presented in Table 1. Second generation adults emerged only in 2022, when 29 out of 131 adults emerged from pupae. No adults were observed to emerge from overwintering pupae after being maintained under outdoor ambient conditions.

Effect of host phylogeny on P. geniculata larval performance

There was no significant effect of the core lineage on pupal weight, though there was a non-significant trend towards lower weights in the core *Sorbus* lineage relative to the Albo-caresinae lineage (F=2.97; df = 1,426; p = 0.086; Figure 9). However, there was a significant effect of subgenus on pupal weight (F= 17.64; df = 3,424; $p < 0.001$). Moreover, the model fit improved relative to the null model (residual deviance = 26.35 vs. null deviance = 29.64), indicating that subgenus explains a meaningful portion of the variation in pupal weight. Post hoc tests revealed that the lowest weights were observed from within the baseline subgenus *Aucupariae*, which did not differ from those within the subgenus *Tianshanicae* (Figure 10). The highest weights were observed when larvae feed within the subgenera *Commixtae* and *Multijugae* (Figure 10).

There was also a significant effect of *Sorbus* species on *P. geniculata* pupal weight (F= 14.13; df = 6,421; $p < 0.001$). Post host tests revealed that the lowest pupal weights were observed when larvae fed on *S. randaiensis* (native to Taiwan), with the next lowest weights observed from its native host, S. *aucuparia*, which did not differ from *S. americana*, *S. cashmiriana*, and *S. gongashanica* (Figure 11). The greatest pupal weights were observed in larvae that fed on *S. microphylla* (native to the Himalayas and China) and *S. decora* (native to eastern North

America) (Figure 11). The relative growth ratios are presented in Figure 12, and show that the relative growth ratio (RGR) differed significantly among *Sorbus* host species ($F = 11.49$; df = 6,421; $p < 0.001$). Using the native host, *S. aucuparia*, as the comparison baseline, larvae reared on *S. decora* exhibited significantly higher RGR (mean difference = 0.793; t = 5.253; $p < 0.001$), as did larvae reared on *S. microphylla* (mean difference = 0.586; $t = 3.211$; $p = 0.024$). Relative growth on *S. gonggashanica* was also greater than on *S. aucuparia*, although this mean difference (0.480) was not statistically significant ($t = 2.468$; $p = 0.174$). In contrast, larvae reared on *S. randaiensis* tended to have lower RGR than those on *S. aucuparia* (mean difference = −0.507; $t = -2.316$; $p = 0.239$), although this effect was not significant. No significant difference in RGR was detected between *S. aucuparia* and either *S. americana* ($t = -0.507$; $p = 0.998$) or *S. cashmiriana* ($t = 0.726$; $p = 0.991$). Overall, these results indicate that larval growth performance was enhanced on two evolutionarily-naïve *Sorbus* species relative to the evolutionarily-native host, which are native to eastern North America (*S. decora*) and East Asia (*S. microphylla*).

Discussion

Larval performance of *P. geniculata*, based upon pupal weight, differed significantly among *Sorbus* taxa at both the species and subgenus levels, indicating that host plant identity and evolutionary relatedness influence larval development. It also suggests that these host plant associated differences likely reflect differences in foliar quality, including nutritional composition, secondary chemistry, leaf toughness, and/or other physiological traits affecting nutrient acquisition and larval growth. Similar host-mediated effects on insect performance have been documented in other herbivorous insects, where plant quality strongly influences larval growth, developmental success, and adult fitness (Awmack & Leather 2002, Stiling & Moon

2005, Salgado & Saastamoinen 2019). Because larger pupal size is frequently associated with increased adult fitness, including greater fecundity, greater hatch success, increased longevity, and increased dispersal capacity (Leather 1993, Honěk 1993), the greater pupal weights observed on several evolutionary-naïve *Sorbus* hosts suggest that these provide comparatively favorable developmental conditions for *P. geniculata*. Conversely, reduced pupal weights on other evolutionary-naïve hosts, such as *S. randaiensis*, may indicate lower nutritional suitability or stronger plant defensive responses that constrain larval performance.

Despite the ability of *P. geniculata* to cause severe or complete defoliation of individual trees, larval feeding rarely appears to cause host tree mortality. Forbes and Daviault (1964) observed no mortality of *S. aucuparia* attributable to repeated defoliation by *P. geniculata*, even after multiple years of feeding damage. They proposed that this resilience was related to the growth phenology of the host and the seasonal timing of larval feeding. In their study, fourth and fifth instars of the first generation occurred primarily between early July and early August, after trees had already completed approximately 50–75% of annual radial growth. As a result, foliage loss occurred relatively late in the growing season, allowing host trees the time needed to replenish carbohydrate reserves following defoliation. Similar phenology was observed in Seattle during the present study, where first instars appeared in late May to early June during 2022–2024. The relatively late timing of feeding may therefore contribute substantially to host tolerance from repeated defoliation. *Sorbus* species may differ in timing of cambial growth, allocation to storage reserves, or timing of photosynthetic recovery after defoliation, and species that complete more growth before defoliation may better tolerate herbivory. Additionally, autumn phenology also varies among *Sorbus* species, and earlier senescence shortens the photosynthetic season, which may reduce the ability of trees to recover carbohydrate reserves following defoliation.

The influence of *Sorbus* evolutionary history on *P. geniculata* larval performance appeared measurable but comparatively weak relative to patterns reported for more destructive invasive herbivores. Previous work examining the role of evolutionary history between evolutionarily-native and evolutionarily-naïve host plants, and invasion severity, reported that the strongest phylogenetic effects are associated with invasive insects capable of causing population-level host mortality (Mech et al. 2019, Uden et al. 2022, Schulz et al. 2025). In contrast, because *Sorbus* species generally tolerate defoliation by *P. geniculata*, and rarely if ever are killed, selective pressure for the evolution of highly specialized defensive chemistry against *P. geniculata* may be reduced, potentially weakening phylogenetic signals in host susceptibility. It is also possible that *Sorbus* species that are considered to be evolutionarily naïve to *P. geniculata* still retain sufficient defenses, possibly shaped by interactions with congener species of *Pristiphora* or related species within Tenthredinidae in their native ranges. For example, there are >130 species within *Pristiphora*, which are globally distributed across the holarctic realm, overlapping with the global distribution of *Sorbus*. *Pristiphora* and the closely related genus *Nematus* contain many host-specialized rosaceous feeders, and plant host shifts among rosaceous genera are relatively common in nematine sawflies (Nyman et al. 2006). Therefore, even if a *Sorbus* species is evolutionarily naïve to *P. geniculata* specifically, it may still possess defenses retained from interactions with other rosaceous-feeding sawflies. Host distribution patterns may further limit the ecological impact and spread of *P. geniculata*. In many forest systems, *Sorbus* species occur as scattered or low-density components of mixed stands rather than forming extensive contiguous populations. Such fragmented host distributions can reduce host connectivity and create spatial barriers between suitable hosts, which can impede the establishment of new colonies and slow the rate of spread (Lampert & Liebhold 2026). Therefore, fragmented

populations of *Sorbus* across landscapes in North America will likely slow the invasion of *P. geniculata* due to reduced host availability.

High larval mortality observed during the study was consistent with earlier observations by Forbes and Daviault (1964), who reported approximately 87% mortality in *P. geniculata*, primarily during the first instar. In the present study and across all *Sorbus* species, a total of 430 larvae out of 1,786 successfully reached the pupal stage, resulting in 75.9% mortality. Also, in this study, mortality was likely reduced by the experimental design in which feeding containers were screened to limit mortality from predators and parasitoids. Also, in the present experiment, fresh foliage was periodically placed directly onto depleted foliage, whereas Forbes and Daviault (1964) used intact trees that required larvae to disperse further to locate suitable feeding sites. Thus, the present study may have induced increased larval crowding and possible pathogen transmission relative to the study reported by Forbes and Daviault (1964). Regardless, both the current and previous study indicate high rates of larval mortality in *P. geniculata*, which is typical of the survivorship dynamics of most insect species (Carey 2001).

The failure of adults to emerge following overwintering was unexpected and unfortunate, and I surmise that it could have been due to dry soil conditions within the containers. Soil moisture strongly influences successful pupation and adult emergence in many soil-pupating insects, and extremely low moisture levels can inhibit completion of development (Li et al. 2019). Under natural conditions, overwintering *P. geniculata* pupae are subject to precipitation and snow cover in the soil layer, whereas in the current experiment, the containers might not have afforded pupae with the same conditions, even though the objective of limiting loss to natural enemies was likely achieved. Future studies aiming to measure overwintering success should account for optimal environmental conditions while limiting the effects of natural enemies.

This study also provides several new host records for *P. geniculata*, including *S. microphylla*, *S. randaiensis*, *S. gonggashanica*, and *S. cashmiriana*. Field observations additionally documented larval feeding on *S. aucuparia*, *S. decora*, *S. scopulina* var. *cascadensis*, *Sorbus* 'Birgitta', and *Sorbus* × *splendida*. Although larvae were observed feeding on *S. scopulina* var. *cascadensis*, *Sorbus* 'Birgitta', and *Sorbus* × *splendida*, successful completion of the life cycle on these plant hosts was not confirmed. Identification of susceptible *Sorbus* species and cultivars is particularly important for *ex situ* conservation collections and botanical gardens, especially because numerous *Sorbus* species are considered vulnerable, threatened, endangered, or critically endangered within their native ranges (IUCN 2025). At the same time, *Sorbus* remains taxonomically and ecologically understudied, with many species lacking formal conservation assessments. International and domestic nursery trade was suspected as a pathway for the initial introduction and subsequent spread of *P. geniculata* in North America (Forbes & Daviault 1964), and continued movement of ornamental stock may pose a risk to vulnerable or geographically restricted *Sorbus* populations. Identification of highly susceptible species could therefore assist monitoring efforts and guide preventative management strategies aimed at reducing the likelihood of introduction into sensitive conservation collections or natural populations.

Collectively, these findings demonstrate that host plant taxonomy substantially influences larval developmental performance in *P. geniculata* and that these effects are structured across both species and subgenus boundaries within *Sorbus*. The results support the hypothesis that host-associated larval performance is linked, at least in part, to evolutionary relationships among host taxa (Mech et al. 2019, Uden et al. 2022, Schulz et al. 2025), even in an insect herbivore that does not cause population-level mortality in its host plants. Future studies integrating foliar nutrient profiles, effects of constitutive and induced plant defenses, and phylogenetic

comparative approaches would help clarify the specific host traits underlying variation in *P. geniculata* developmental success.

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Tables

Table 1-1: Counts of *P. geniculata* larvae (introduced) and pupa (recovered) from experimental buckets in 2022, 2023, and 2024.

	2022		2023		2024		Total	
Species	Introduced	Recovered	Introduced	Recovered	Introduced	Recovered	Introduced	Recovered
S. americana	162	72	88	8	98	4	348	84
S. aucuparia	44	28	88	4	88	15	220	47
S. decora	223	72	82	20	86	12	391	104
S. randaiensis	77	13	91	13	108	6	276	32
S. gonggashanica	24	23	81	14	121	3	226	40
S. cashmirana	-	-	96	71	88	7	184	78
S. microphylla	-	-	-	-	141	45	141	45

Figures

Figure 1-1: Defoliation of *Sorbus scopulina* var. *cascadensis* caused by *P. geniculata* larval feeding.

Figure 1-2: *Pristiphora geniculata* larvae gregariously feeding on *Sorbus* foliage.

Figure 1-3: Preliminary rearing trial. Four 3.8-liter glass jars with 2.54 cm of sandy soil with *Sorbus* foliage and *P. geniculata* larvae added.

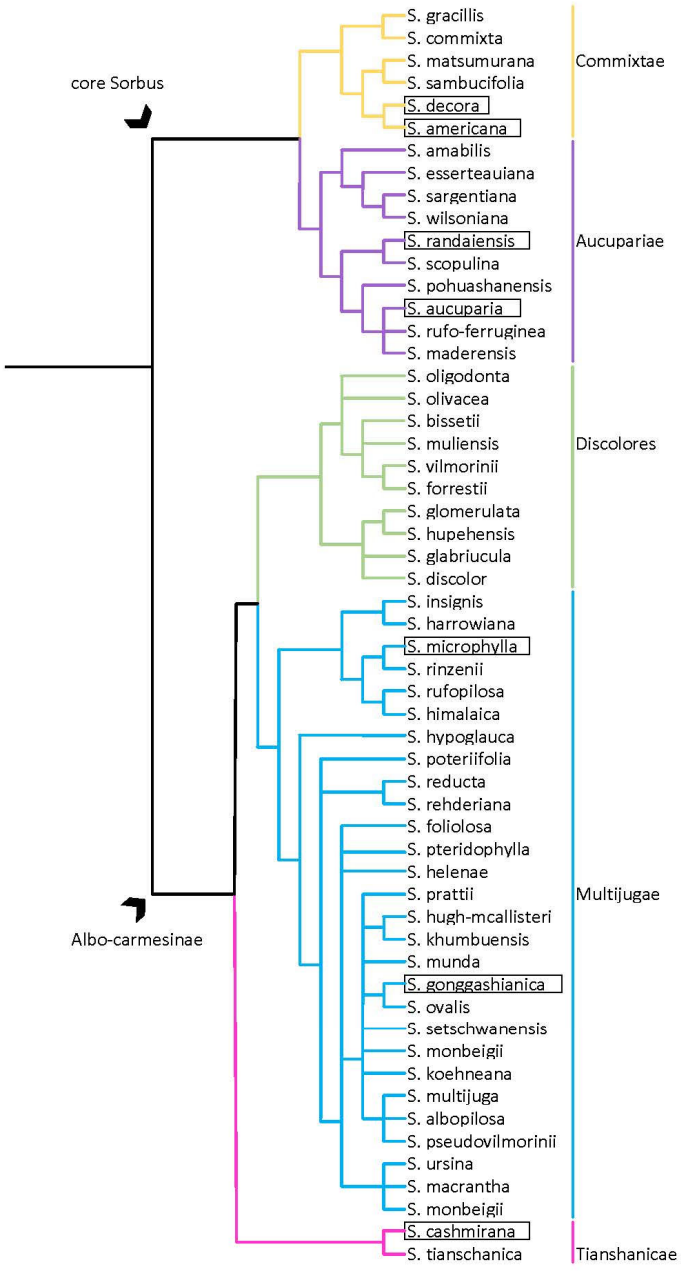

Figure 1-4: Compiled phylogenetic tree of *Sorbus* spp. based on analyses done by Li et al. (2017), Lo and Donoghue (2012), and Garrison (unpublished data, Fig. 5). Arrows indicate core lineages, colored bars on the right indicate subgenera, and boxed species indicate species used in this study.

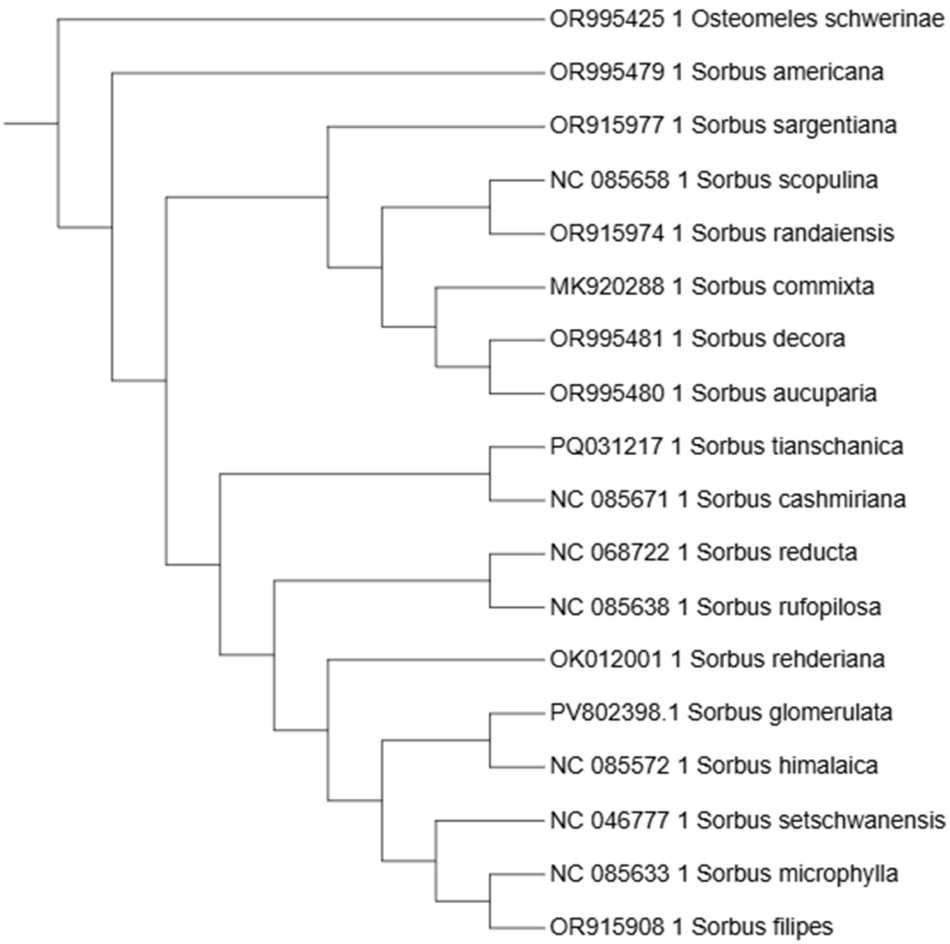

Figure 1-5: Evolutionary analysis of *Sorbus* species by the Maximum Likelihood method to determine the position of *Sorbus randaiensis.*

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Figure 1-6: Experimental setup for 2022. Three replicated ~7.6 L buckets for 13 *Sorbus* species. Each bucket contained a 25mm deep layer of soil.

Figure 1-7: Floral tube filled with water and *Sorbus cashmiriana* foliage inserted.

Figure 1-8: Adult *P. geniculata* on *Sorbus* 'Birgitta'.

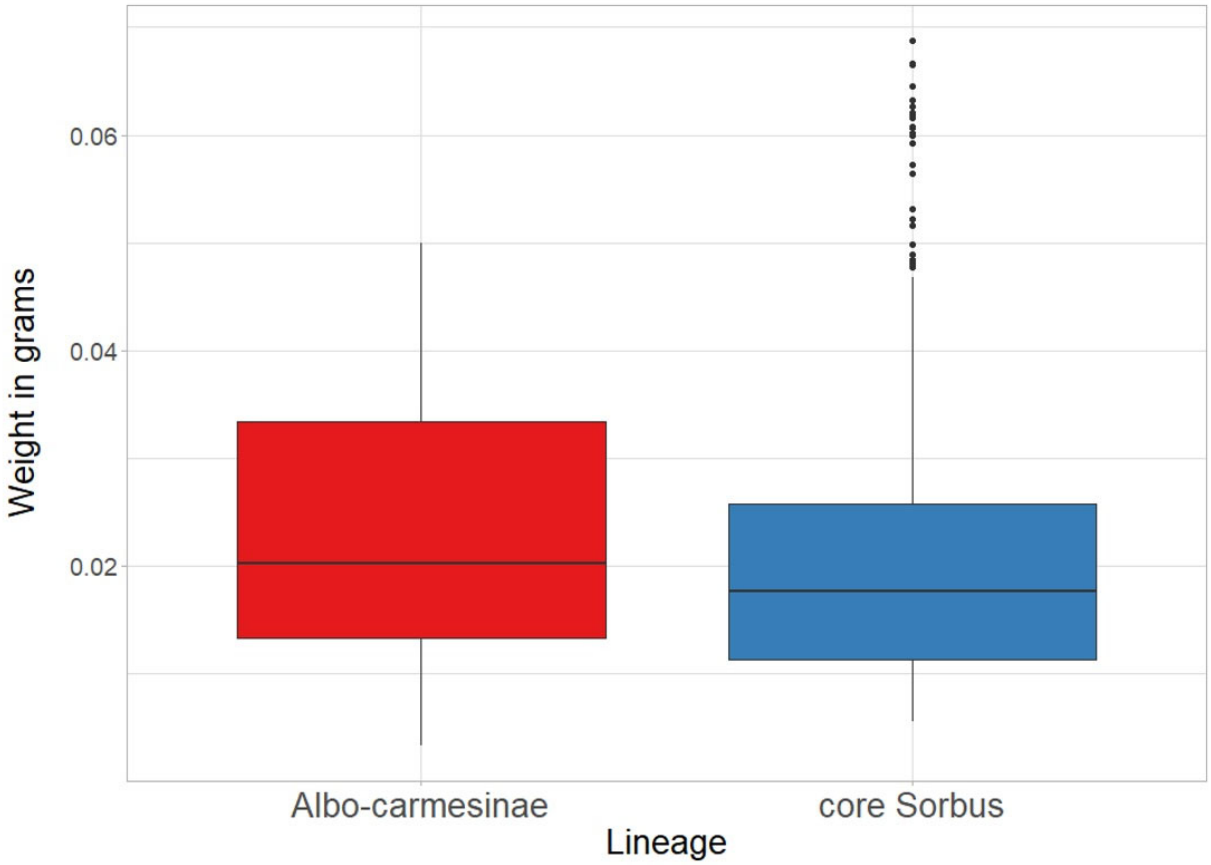

Figure 1-9: Boxplots of the weight of *P. geniculata* pupa across *Sorbus* lineage.

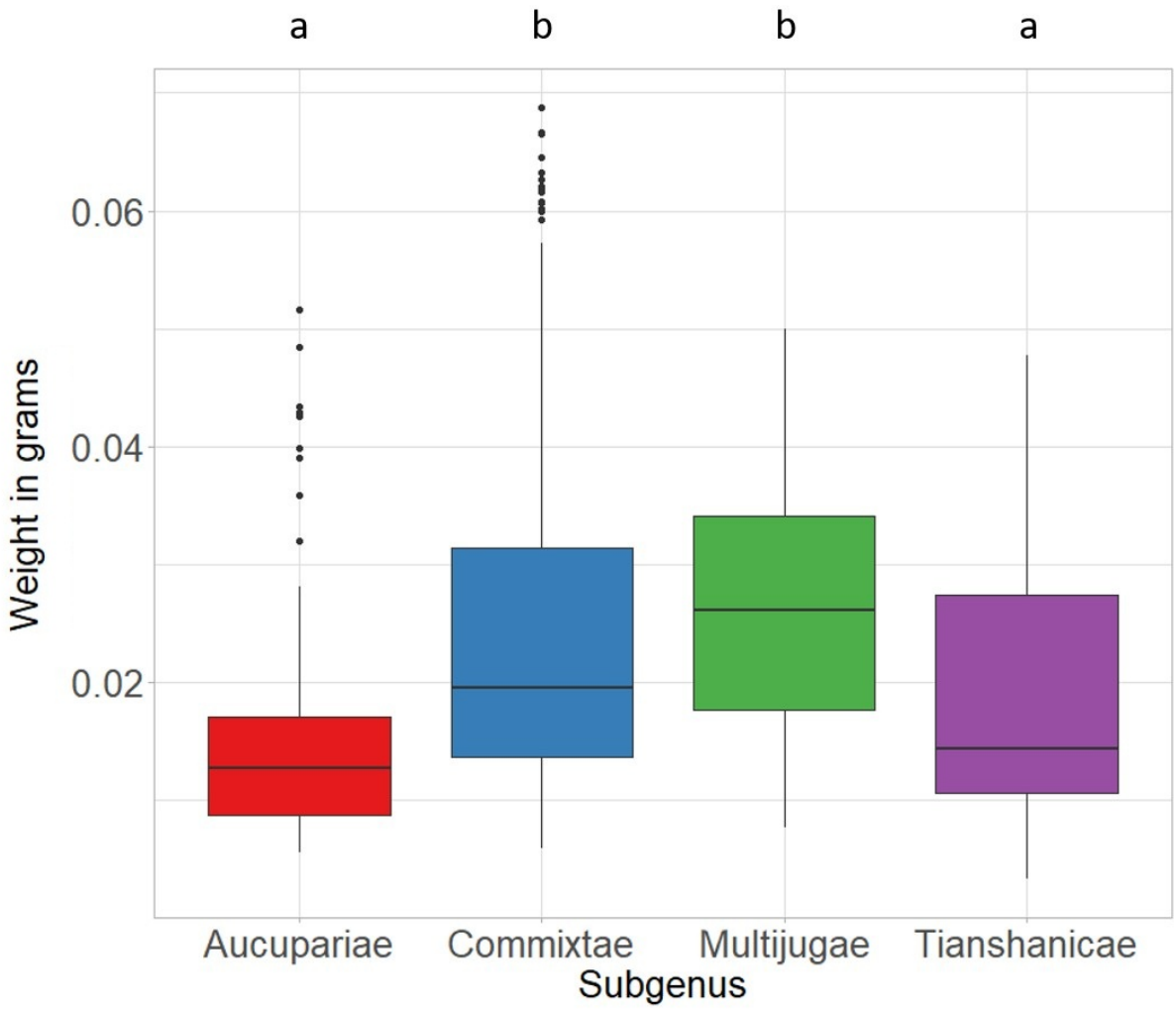

Figure 1-10: Boxplots of *P. geniculata* pupal weight across *Sorbus* subgenera. Different letters indicate significant differences among species based on Tukey HSD post hoc comparisons (family-wise $\alpha = 0.05$).

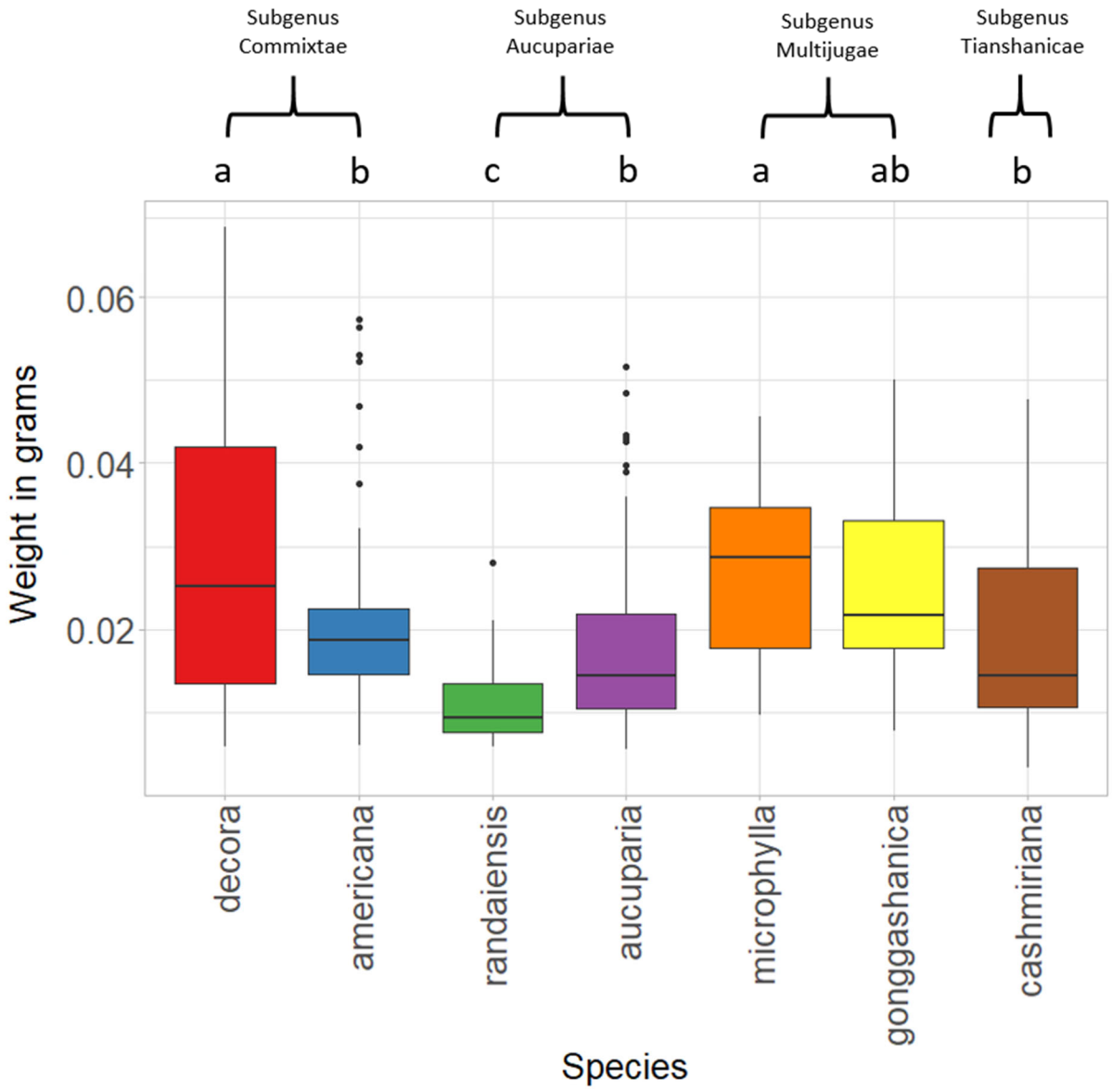

Figure 1-11: Boxplots of the weight of *P. geniculata* pupa across *Sorbus* species. Different letters indicate significant differences among species based on Tukey HSD post hoc comparisons (family-wise $\alpha = 0.05$). The corresponding subgenus of each species is noted at the top of the figure.

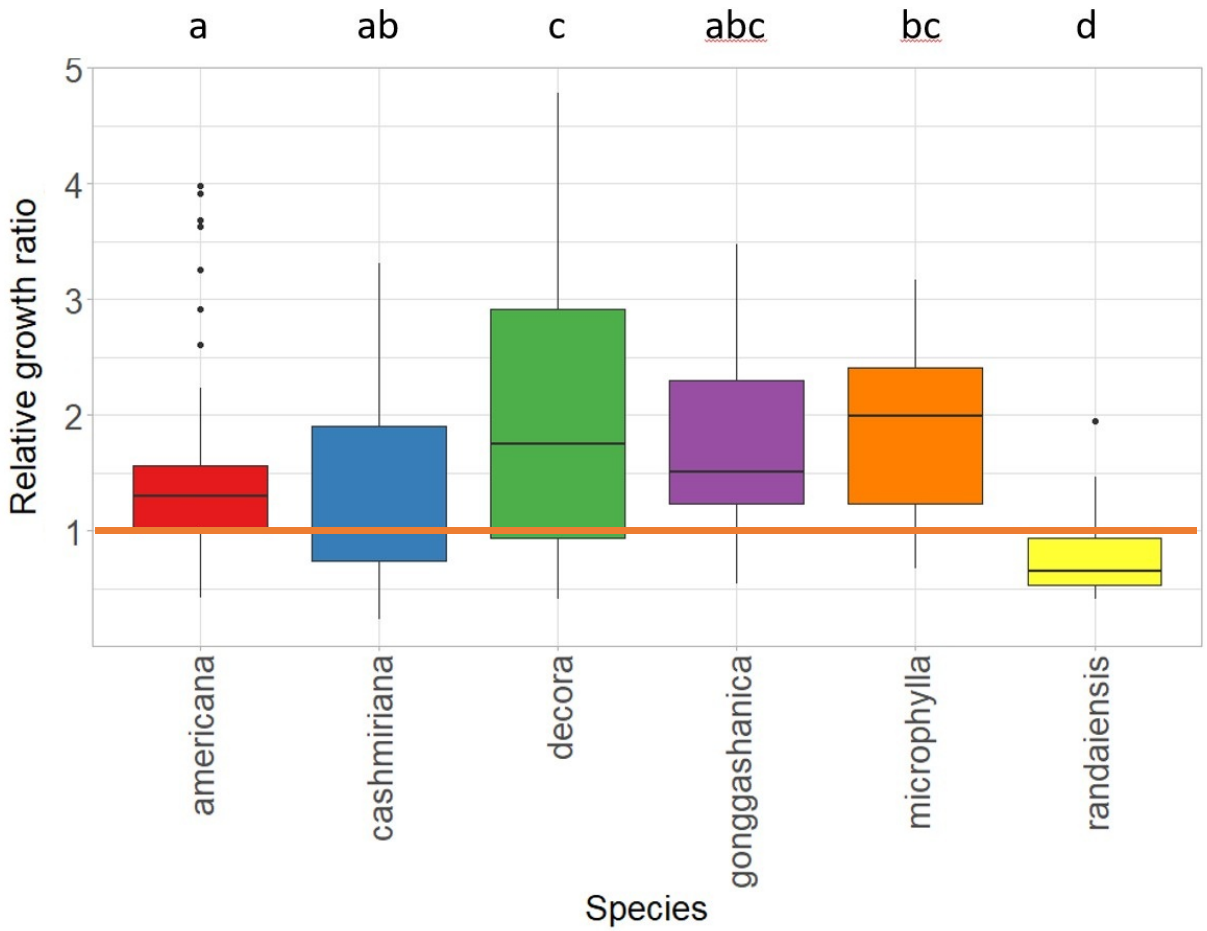

Figure 1-12: Boxplots of the relative growth rate of *P. geniculata* pupa across *Sorbus* species to *S. aucuparia*. Different letters indicate significant differences among species based on Tukey HSD post hoc comparisons (family-wise $\alpha = 0.05$). The orange line highlights the Relative growth ratio of *S. aucuparia* (1).

Chapter 2 The role of host phylogenetic history and climate on *Enarmonia formosana (Scopoli)* and *Monilinia* spp. brown rot on *Prunus* spp.

Abstract

The genus *Prunus* L. (Rosaceae) comprises over 200 species of deciduous and evergreen trees and shrubs that are of substantial ecological, horticultural, and economic importance worldwide. Members of the genus include globally significant fruit and nut crops such as peaches (*P. persica*), plums (*P. domestica*, *P. cerasifera*, *P. americana*), apricots (*P. armeniaca*), almonds (*P. dulcis*), and cherries (*P. avium, P. cerasus*), in addition to widely cultivated ornamental flowering cherries and timber species such as black cherry (*P. serotina*). In the Pacific Northwest, *Prunus* species are especially prominent in urban forestry, botanical collections, and managed landscapes. The Washington Park Arboretum in Seattle, Washington, maintains extensive *Prunus* plantings, including culturally and ecologically significant displays along Azalea Way, while the urban forest of Seattle contains numerous cherry trees. Despite their aesthetic, cultural, and ecological value, *Prunus* species are among the most intensively managed trees in the region due to their susceptibility to invasive insects and fungal pathogens. Two particularly important threats include the non-native cherry bark tortrix (*Enarmonia formosana*), a cambium-feeding moth that causes dieback and progressive structural decline, and *Monilinia* spp. (notably *M. fructicola* and *M. laxa*), fungal pathogens responsible for brown rot disease affecting blossoms, twigs, and fruit under favorable environmental conditions.

In this chapter I tested the hypothesis that susceptibility in *Prunus* is jointly structured by evolutionary lineage and climatic context. Specifically, I predict that taxa lacking shared evolutionary or biogeographic history with these pests and pathogens, and those grown under climatic conditions that favor pest or pathogen development, will experience higher levels of damage and disease severity. In contrast, species originating from regions with analogous climatic regimes or historical exposure to similar biotic stressors are expected to exhibit greater tolerance or reduced susceptibility. This framework allows for evaluation of both phylogenetic signal and climate-mediated effects in shaping host vulnerability across diverse Prunus taxa.

Field surveys were conducted from 2016 to 2025 during the fall season, with 169 to 174 *Prunus* individuals inspected annually to record severity of *E. formosana*, severity of cherry brown rot, and tree condition. Data were analyzed across several explanatory variables including climate history, host age, cultivar versus species status, phylogenetic subgenus, and geographic origin. I observed that *Prunus* susceptibility to both *E. formosana* and brown rot, as well as overall tree condition, was jointly structured by host phylogeny, geographic origin, and seasonal climate variables. *Enarmonia formosana* severity was most strongly associated with late-winter minimum temperatures and early spring warming, indicating strong sensitivity to overwinter survival and early phenology. Brown rot severity was primarily associated with spring precipitation frequency and warm summer conditions, consistent with moisture-driven infection dynamics and temperature-dependent pathogen growth. Tree condition was most strongly influenced by early spring precipitation, reflecting cumulative stress during budbreak and early growth periods. Both *Monilinia* brown rot and *E. formosana* infestation contribute to declining tree condition, although brown rot severity appears to be the dominant driver of poor condition.

The results of this chapter should inform integrated pest management (IPM) strategies for botanical gardens, arboreta, and urban forestry programs by identifying *Prunus* taxa at elevated risk under both current and changing climatic conditions. Given the large number of *Prunus* individuals in managed landscapes, including extensive municipal plantings, improved understanding of risk structure has direct implications for monitoring efficiency, maintenance prioritization, and long-term landscape resilience. More broadly, this study also demonstrates the value of combining long-term horticultural monitoring datasets with high-resolution climatological records and curated public garden collections to address ecological and evolutionary questions.

Introduction

Prunus L. (Rosaceae) consists of over 200 species of deciduous and evergreen trees and shrubs with several members that are economically important timber, fruit and nut crops (Chin et al. 2014, Shi et al. 2013). This genus is characterized by simple leaves with stipules and leaf glands, a superior single ovary, and drupe fruits (Liu et al. 2013). *Prunus* is valued for its food products from cultivated species such as peaches (*P. persica* (L.) Batsch), plums (e.g., *P. domestica* L., P. cerasifera Ehrh., *P. americana* Marshall), apricots (*P. armeniaca* L.), almonds (*P. communis* (L.) Huds.) and cherries (e.g., *P. avium*, *P. cerasus*) (Shi et al. 2013). Flowering cherries of section Pseudocerasus Koehne (subgenus Cerasus Pers.) are widely planted ornamentals (Ingram 1948), and a few species, such as black cherry (P. serotina Ehrh.), are valued for timber (Marquis 1990). The genus is widely distributed both in the temperate zone of the Northern Hemisphere and in the subtropical and tropical forests of Asia, Africa, South America and Australia (Rehder 1940, Kalkman 1965, Chin et al. 2014).

Prunus belongs to the subfamily Amygdaloideae, which differs from other rosaceous subfamilies by having a drupe, a fleshy fruit with a stony endocarp or stone (de Candolle 1813). *Prunus* was traditionally classified into 5 or 6 main subgenera based on fruit and bud morphology: *Amygdalus* (peaches/almonds), *Prunus* (plums/apricots), *Cerasus* (cherries), *Padus* (bird cherries), *Laurocerasus* (cherry laurels), and *Emplectocladus* (desert almonds) (Rehder 1940). Molecular phylogenetic studies of *Prunus* using plastid (*trnL-L-F*, *ndhF* and *trnS-S-G*) and nuclear ribosomal ITS (*nrITS*) sequences have supported the monophyly of the genus (Bortiri et al. 2001 & 2006, Chin et al. 2014; Lee & Wen 2001, Shaw & Small 2004, Wen et al. 2008) and shown that the genus *Maddenia*, with only five Asian species, is included (Chin et al. 2010; Liu et al. 2013). However, these studies also refuted previous circumscriptions of subgenera, which

were all shown to be either paraphyletic or polyphyletic, with the exception of subgenus *Emplectocladus*. Three distinct clades were discerned by the concatenated four-gene plastid dataset and designated according to inflorescence structure, as 'Solitary', 'Corymbose' and 'Racemose', and seven sections were further subdivided within these clades (Shi et al. 2013, Chin et al. 2014). The three major clades resolved under *Prunus* s.l. are treated to be three subgenera. Clade I (subgenus *Padus*) have flowers arranged of racemes and consists of species belonging to groups *Laurocerasus*, *Maddenia*, *Padus,* and *Pygeum*. Clade II (subgenus *Cerasus*) have a corymbose flower, and includes the true cherry species and two species that were previously treated as bird cherries. Clade III (subgenus *Prunus*) have a solitary flower and includes almonds, apricots, dwarf cherries, peaches, and plums (Bortiri et al. 2001, Shi et al. 2013, Chin et al. 2014, Zhang et al. 2017).

The biogeographic origin and rapid diversification of Rosaceae occurred during the Cretaceous in North America ~86 million years ago (MYA), and the ancestor of Amygdaloideae was present in North America in the Paleocene shortly after the K-T extinction event (65 MYA) (Chin 2012). From the Late Cretaceous to the Middle Eocene, the climate in the Northern Hemisphere was much warmer and more humid than today (Morley 2000). The ancestor clade of what would eventually become *Prunus* was a component of a continuous belt of forest known as the Boreotropical forest or the Northern Megathermal forest from Asia to North America across the Beringia (Wolfe 1975, Morley 2000). Divergence of *Prunus* was estimated to occur between 56.7 and 67.4 MYA in eastern Asia and diversification of all major lineages was assumed to have been triggered by the global warming period of the early Eocene (Chin 2012). The diversification between the Paleocene and Miocene suggests that paleoclimatic events were an important driving force for *Prunus* diversification (Su et al. 2023). Floristic exchanges between

North America and Eastern Asia could have occurred by either the North Atlantic Land Bridges or the Bering Land Bridge (Chin 2012). Analyses suggest that the most likely ancestral area for the ancestor of Amygdaloideae was western North America; this implies the dispersal of 'proto-*Prunus*' from western North America to Eastern Asia was most likely via the Bering Land Bridge (Chin 2012). The likelihood of the Bering Land Bridge as the main dispersal corridor is also supported by the high density of basal lineages of Amygdaloideae such as Lyonothamnus, Physocarpus, Neviusia, and Oemleria in Western North America (Chin 2012).

Azalea Way, the most iconic feature of the Washington Park Arboretum (WPA), was developed beginning in the late 1930s, and is a key feature of the original Olmsted Brothers design (UWBG 2019). This 1.2 km path through the heart of the Arboretum features azaleas, flowering cherries, dogwoods, magnolias, and companion plants, set against a backdrop of evergreen trees and second growth conifers. Of all these plants, the cherries (*Prunus* spp.) require the most time and resources from the horticultural staff to maintain. *Prunus* spp. are host to a variety of fungal, bacterial, and insect pests that threaten their health (Pscheidt and Ocamb 2020). Cherry trees also constitute a large part of other public and private landscapes in the area, and there are over 33 thousand cherry trees inventoried in the City of Seattle alone (City of Seattle 2026). Important threats to their health include a non-native insect, cherry bark tortrix, *Enarmonia formosana* (Scopoli) (Lepidoptera: Tortricidae), and a fungal pathogen that causes cherry brown rot (*Monilinia fructicola* Wint. and *Monilinia laxa* Aderhold & Ruhland).

Cherry Bark Tortrix, Enarmonia formosana (Scopoli)

Enarmonia formosana is native to Europe, Asia, and northern Africa, and is a reported pest of trees in the rose family (*Rosaceae*) (Van der Geest & Evenhuis 1991). It seems to prefer trees in

the subfamily *Amygdaloideae*, which includes the genera *Prunus*, *Malus*, and *Sorbus* (Jenner et al. 2004). It was first mentioned as a pest of almond and stone-fruit trees in Europe by Kollar (1837), and since then it has been noted for sporadic, local outbreaks in its native range (Massee 1954; Smol'yannikov 1979; Dobroserdov 1981). In 1989 a homeowner in British Colombia, Canada, reported cherry trees exhibiting symptoms of yellowing foliage and bark damage that included cankers, gummosis and frass, and *E. formosana*, was positively identified based on detailed examinations of these specimens (Dang & Parker 1990). It is believed that *E. formosana* has been in the British Columbia area for some time, based on the size of lesions on the host trees from repeated infestations of larvae, and from the large number of adults caught in pheromone traps set in these areas during the summer of 1990 (Dang & Parker 1990). Subsequently, *E. formosana* has established itself as a key pest of ornamental cherries in cities along the Pacific Coast of North America (Klaus 1992). The WPA has prominent gardens featuring the host trees of *E. formosana*, including *Prunus* spp. along Azalea Way, *Malus* spp. in the Crabapple Meadow, and the Brian O. Mulligan *Sorbus* collection. As the common name of the insect implies, *Prunus* is the genus most often infested in the Arboretum, with *Malus* being infested occasionally and *Sorbus* attacked rarely (Garrison, unpublished data).

Enarmonia formosana is a species in Tortricidae, commonly known as the leafroller moths and one of the largest families of Lepidoptera with over 10,000 described species (Royals et al. 2016). Various morphological aspects of the species, including illustrations and/or photographs, can be found in Benander (1950), Bradley et at. (1979), Graaf Bentinck and Diakonoff (1968), Hannemann (1961), Kennel (1921), Kuznetsov (1978), and Pierce and Metcalfe (1922). *Enarmonia formosana* can be recognized by the intricately well-defined colors and patterns of the forewing and unique structures of male and female genitalia. The distinctive forewing length

is between 7.0-9.0 mm and the pattern consists of a black ground-color and silver and yellow markings with three conspicuous parallel black bars that form the “eye spot” near the end of the wings (Royals et al. 2016). There is little morphological variation or sexual dimorphism in this species.

Enarmonia formosana spends most of its life as a larva mining between the bark and cambium of the host tree (Breedveld & Tanigoshi, 2007). Based on flight activity, *E. formosana* is described as both univoltine and bivoltine (Roediger 1956, Sermann and Zahn 1986, Tanigoshi and Murray 2000). In Seattle, adult *E. formosana* are active from April to September (Beers et al. 1993). Adults oviposit singly or in groups near tree wounds, cankerous growths, graft unions, or enlarged lenticels (van der Geest & Evenhuis 1991). After hatching, first instars feed on the bark and outer sapwood while the 2nd through 5th instars tunnel between the bark and cambium. During winter and spring, *E. formosana* is mostly dormant as late instars within the bark, but will feed throughout the winter months when temperatures are above freezing. In early spring (~March), late instars pupate and emerge as adults later in the spring. *Enarmonia formosana* feeding girdles sections of the tree causing dieback of new and old growth. Feeding by *E. formosana* also weakens the tree, making it susceptible to secondary issues such as bark beetles, freezing damage, or fungal pathogens.

Monilinia spp. Brown Rot

Plant pathologists and mycologists often use the term ‘brown rot' in a very general sense to describe a variety of plant diseases that may be caused by fungi, bacteria, or physiological disorders (Byrde & Willetts 1977). At the WPA, brown rot has been used in a more restricted sense, specifically referring to a group of fungal pathogens that cause damage to cultivated fruit

and ornamental trees, particularly apples, pears, and stone fruit from temperate areas of the world (Byrde & Willetts 1977). This fungal group, within the genus *Monilinia*, is an important ascomycete pathogen within the Helotiales order. There are more than 30 described species of this genus. Among them, three species (*Monilinia fructicola* (G. Winter) Honey, *Monilinia fructigena* (Pers.) Honey and *Monilinia laxa* (Aderh. & Ruhland) Honey) are known for being particularly aggressive, generating important economic losses (Huang et al. 2021, De Miccolis Angelini et al. 2022). These pathogens are capable of infecting a wide variety of tissues and organs, generating different symptomatologies depending on the plant host (Holb & Scherm 2008).

Monilinia fructigena is widespread in Europe, Asia, northern Africa, and some parts of South America, but is not known to be established in North America, Australia and New Zealand outside of quarantined conditions (Landi et al. 2018). It causes one of the most important diseases on pome fruits, especially on apple and pear where it primarily causes fruit rot before and after storage and marketing (Jones and Aldwinckle 1990, Hrustić et al. 2012). *Monilinia laxa* is thought to be native to Europe where it was first identified as the causal agent of brown rot on stone fruit (Byrde & Willets 1977, Papavasileiou et al. 2015). *Monilinia laxa* has been established in North America for quite some time and was a prevalent species on peach, nectarine, apricot, and cherry in California (United States) in the first half of the 20th century (Hewitt & Leach 1939). It is an economically important fungal pathogen of stone fruits, causing mainly blossom and twig blight, and has also been detected on pome fruits (Byrde & Willetts, 1977). *Monilinia fructicola* is mainly a blossom, twig, and fruit pathogen of stone fruits that is assumed to be native to North America (Fulton, 1999, Muñoz et al., 2008). It is the main agent of the disease in North and South America, and has also been reported in Australia, China, Japan,

and more recently Europe (Papavasileiou et al. 2015). *Monilinia fructicola* and *M. laxa* are the organisms associated with brown rot in Washington State (Pscheidt & Ocamb 2026). The disease is more of a problem west of the Cascade Range, and surveys of eastern Washington packinghouses during 2000 and 2001 found very little brown rot on peaches and nectarines (Holb and Schnabel 2005). Under favorable weather conditions, the disease caused by these pathogens develops rapidly, and heavy rains during the period of blooming as well as temperatures ranging from 20 to 25°C during the day and cold nights are ideal conditions for pathogen spreading (Hrustic et al. 2012).

Hypotheses

I hypothesize that *Prunus* spp. from different subgenera and different native regions will differ in their responses to *E. formosana* and *Monilinia* spp., the causative agent of cherry brown rot, due to the presence or absence of shared evolutionary history. Specifically, *Prunus* from areas where the plant, insect, and/or disease have coevolved would have a tolerance for the insect or disease, and *Prunus* that have not coevolved with this relationship would be susceptible to severe damage. A secondary goal of this project is to provide needed information to inform Integrated Pest Management strategies aimed to protect and conserve *Prunus* spp. that are maintained within botanic gardens, arboreta, and other public spaces. Lastly, this project also demonstrates the usefulness of data collected by professional public garden staff in answering important scientific questions about public plant collections, which are threatened by complex issues (Smith 2019).

Materials and Methods

Study Site

This study was conducted at the Washington Park Arboretum in Seattle, Washington (47° 38' 28.32" N, 122° 17' 36.996" W). The Washington Park Arboretum is located in the Puget Sound Basin with downtown Seattle directly southwest, the University of Washington to the northwest, and Lake Washington directly east. The 0.93 km^2 park occupies most of a long narrow glacial ravine running north and south with the northern most tip touching Union Bay (Ion 2003). The plant collections include over 14,500 accessioned specimens in the collections; over 4,000 different types of trees, shrubs and other plants native to 98 countries, which serve as vital resources for scientific study (UWBG 2019). The University of Washington Botanic Gardens maintains the plant records at the Washington Park Arboretum in BG-BASE (O'Neal 2019), a database application designed to manage information on biological (primarily botanical) collections, and the plants are mapped using ArcGIS Pro (ESRI 2019). The Arboretum currently has 163 individual records for living trees in the genus *Prunus*.

Data Collection

Prunus trees were examined in the fall (September – October) annually from 2016 to 2025. This time window was chosen because it is when brown rot symptoms are most detectable, occurring before leaf drop when dead leaves, mummified flowers and fruit, and twigs/branch cankers are highly visible. Additionally, during this time, *E. formosana* are still actively feeding in the larval stage, resulting in detectable and new frass tubes. In each year, 169 -174 individual *Prunus* trees

were inspected; the year-to-year variability in the number of inspections was due to tree removal due to poor health/ hazardous trees, and new plantings. Beginning in 2019, plants in the genus *Malus* (n=75) and *Sorbus* (n=120) (senso lato) were also inspected for *E. formosana*. Data for *Malus* and *Sobus* were not used in any analysis, but was done to confirm reports in literature that *E. formosana* feeds on most members of subfamily Amygdaloideae, and these genera are major collections within the University of Washington Botanic Gardens. Data were collected using the ArcGIS Collector application (ESRI 2025) until 2022 when the application was replaced by the ArcGIS Field Maps app. Over the 10-year sampling period, a total of 1,412 observations, or tree-years, were recorded.

Response variables

To detect *E. formosana*, I inspected the base of each tree, its stem up to ~2m, and its lower branches (within ~2 m) using a flashlight. I initially rated the level of infestation on a scale from 0 to 3. A ranking of 0 indicated no frass tubes detected, 1 indicated a minor infestation (i.e., a few (>10) frass tubes found), 2 indicated a moderate infestation (i.e., at least 10 frass tubes detected), and 3 indicated a major infestation (i.e., > 25 frass tubes detected).

Brown rot was also rated according to a scale from 0 to 3. A ranking of 0 indicated no detectable brown rot dieback, a 1 indicated minor brown rot dieback (i.e., sporadic branch section dieback and/or mummified flowers, leaves, and/or fruit), 2 indicated a moderate infection (i.e., entire but sporadic branch dieback and mummified flowers, leaves, and/or fruit), and 3 indicated major brown rot dieback (i.e., widespread branch or sections of canopy dieback including many mummified flowers, leaves, and/or fruit).

Overall plant condition was also evaluated on a scale from poor to excellent. These evaluations were then converted into an ordinal scale, roughly mirroring the scale and format of the *E. formosana* and brown rot ratings. Low numbers indicate a plant in excellent (rating = 0) or good (rating = 1) condition (mirroring low numbers indicating no or low *E. formosana* and brown rot) and high numbers indicating fair (rating = 2) or poor (rating =3) condition (mirroring low numbers for no or little *E. formosana* or brown rot and high numbers indicating severe *E. formosana* or brown rot).

Explanatory variables

For each tree, I recorded the tree age from BG-BASE accession records. If the plant was received as a plant with no indication as to its size, or if it was received as seed or scion material, the date received was used as the "birth" date. If the plant was received as a plant with size data, 3 years were added to the age to account for the likely number of years in the nursery. Each tree was also categorized based on whether it was a cultivar or species. This was to test if cultivated varieties, often bred for flower abundance or size, would differ in their susceptibility to brown rot.

The geographical origin of each species or cultivar was determined by literature review or, if it was directly collected from the wild, from BG-BASE accession records. In the case of a hybrid *Prunus*, the parentage was researched to determine origin. There were no cases where the geographic origin of cultivar parents was in a different category. Five different regions for geographic origin were identified: East Asia, Japan, Southeast Asia, Western Eurasia, Eastern North America. The subgenus was determined from previous phylogenetic studies, specifically Bortiri et al. (2001), Shi et al. (2013), Chin et al. (2014), Su et al. (2023), and Song et al. (2024).

Weather data

Due to the importance of annual weather on *E. formosana* overwintering mortality and spring-to-summer developmental rates, and its effect on fungal pathogens, weather data were obtained from AgWeatherNet, a service of Washington State University, whose mission is to collect and deliver quality spatiotemporal weather data, site-specific forecasts, and drive decision support in crop, human, and animal health systems (AgWeatherNet 2026). Data were obtained from the Seattle weather station located at the Center for Urban Horticulture (47° 39' 25.5594" N, -122° 17' 20.3634" W) and included daily minimum and maximum temperatures, and daily measurements of precipitation (in mm). From these data, I calculated the minimum January temperature and the maximum July temperature as proxies for winter and summer temperature extremes, respectively. I used daily precipitation measurements to determine the total precipitation and frequency of precipitation (days with precipitation > 0) for February, March, and April, which are the months that *Prunus* spp. are in bloom at the study site. I also calculated the average temperature for February, March, and April using daily average temperature measurements.

Statistical Analyses

The ratings for *E. formosana*, brown rot, and tree condition were each converted into a binary response variable. For *E. formosana*, there was a detectable difference between ratings of 0 or 1, where there were no or very few frass tubes found, and 2 and 3, where frass tubes were very prevalent and easy to find all over the trunk. I thus converted ratings of 0 and 1 into a low severity *E. formosana* category, and ratings of 2 and 3 into a high severity *E. formosana*

category. Likewise, with brown rot, there seemed to be a clear delineation between a rating of 0 or 1 where there were no or very little scattered symptoms of brown rot, and 2 or 3 where there was widespread damage throughout the canopy foliage and twigs/branches. As in the case of *E. formosana* ratings, a 0 indicates low severity brown rot, and a rating of 1 indicates high severity brown rot. For overall condition plant rating, a delineation was made between excellent or good where there is no evidence of decline, and fair or poor where there is clear evidence of minor or major decline in tree health. Thus, ratings of poor or fair were coded as 1, and ratings of excellent or good were coded as 0.

Due to the number of biotic and abiotic predictor variables, and the potential for multicollinearity, I first used stepwise regression with the full suite of abiotic predictor variables on each response variable (severity of *E. formosana* and brown rot, coded as 0 or 1, and tree condition rating, coded as poor or good). Additionally, due to the large number of abiotic variables, the multicollinearity between the monthly precipitation variables (frequency and total), and the importance of sustained humidity on brown rot severity, only frequency of precipitation was used. I repeated this process for the full suite of biotic predictor variables, and included biologically relevant interaction effects (subgenus, cultivar/species status, geographic origin, and age). I used the default parameter for *k* in the step () function in R, which uses AIC to keep or discard variables. I also used the mixed stepwise approach, which allowed for variables to enter the model and/or be discarded. Any abiotic and biotic predictor variables remaining from their respective stepwise procedures were then used in the full model for each response variable. Significance of main and interacting effects was based on the likelihood ratio χ^2 using the car package (Fox & Weisberg 2019) in RStudio. Post hoc tests using emmeans (Lenth & Piaskowski 2026) in RStudio were used if categorical predictor variables were found to be significant.

Results and Discussion

Severity of Enarmonia formosana

The stepwise regression approach for the abiotic variables removed minimum January temperature, frequency of precipitation in February, frequency of precipitation in April, and average April temperature. The stepwise regression approach for the biotic variables removed the interactions of subgenus × origin, cultivar status × origin, subgenus × age, and subgenus × cultivar status. The final model yielded a minimized AIC of 1595.0 (Residual Deviance: 1557.0 on 1395 degrees of freedom), down from a Null Deviance of 1766.0 on 1411 degrees of freedom, validating the final model for predicting *E. formosana* severity.

The results of the Type III analysis of deviance analysis of the final *E. formosana* severity model is presented in Table 1A. Relationships between continuous abiotic and biotic predictor variables, and the probability of high severity of *Enarmonia formosanais* is presented in Table 2-4. The final model revealed that *E. formosana* severity was significantly influenced by several phylogenetic, geographic, and climatic variables. Subgenus had a significant effect on severity (LR $\chi^2 = 10.211$, $df = 2$, $p = 0.006$), indicating that the response differed among major taxonomic groups. Specifically, post-hoc pairwise comparisons on the estimated marginal means (Table 1B) revealed that the comparison between *Cerasus* and *Prunus* showed significantly different estimated odds (odds ratio = 2.0, $p = 0.041$), suggesting that taxa within *Cerasus* exhibited approximately twice the odds of the measured response relative to *Prunus*. In contrast, comparisons involving *Padus* were not significant ($p = 0.999$ for both contrasts), indicating substantial overlap in response between *Padus* and the other subgenera.

Geographic origin also significantly affected severity (LR $\chi^2 = 9.990$, $df = 4$, $p = 0.041$), suggesting regional differentiation in response patterns (Table 1C). In addition, plant age was a significant predictor (LR $\chi^2 = 9.031$, $df = 1$, $p = 0.003$) (Figure 4C), as was the interaction between origin and age (LR $\chi^2 = 15.301$, $df = 4$, $p = 0.004$), demonstrating that the effect of age varied among geographic origins. Cultivar versus species status was only marginally significant (LR $\chi^2 = 3.773$, $df = 1$, $p = 0.053$).

Several climatic variables were strongly associated with *E. formosana* severity (Figure 4A, 4B, and 4D). Average March temperature showed the strongest relationship (LR $\chi^2 = 32.157$, $df = 1$, $p < 0.001$), while average February temperature was also highly significant (LR $\chi^2 = 13.207$, $df = 1$, $p < 0.001$). Maximum July temperature had a weaker but still significant effect (LR $\chi^2 = 5.707$, $df = 1$, $p = 0.017$), while the frequency of March precipitation was not significant (LR $\chi^2 = 2.880$, $df = 1$, $p = 0.090$).

Among the climatic variables, spring warming was observed to be a critical factor, with both average February and March temperatures serving as strong predictors of *E. formosana* severity, with each being positively associated with an increased odds of severe infestation. These seasonal temperature effects may reflect sensitivity of developmental or physiological processes to conditions immediately preceding active growth periods (Schebeck et al. 2024). Early spring warming may enhance larval developmental rates and survival, adult fitness, or synchronization with host phenology (Schwartzberg et al. 2014). Temperature-driven increases in insect development and outbreak severity are well documented in forest insects and are frequently linked to climate warming trends (Bale et al. 2002; Bentz et al. 2010).

Geographically, trees with lineages originating from Japan and Southeast Asia showed high probabilities for severe *E. formosana* infestation. Host age had a positive effect on infestation

severity overall, although this relationship varied significantly among origins, as indicated by the significant origin × age interaction. In particular, the negative interaction term for Southeast Asian taxa entirely overrides the positive global main effect of age on infestation for taxa from that region.

Enarmonia formosana infestation severity was strongly structured by host phylogeny. The highly significant effect of subgenus suggests that evolutionary relationships among host taxa influence susceptibility to infestation. Taxa within *Prunus* exhibited lower infestation severity relative to *Cerasus*, indicating that host lineage may mediate bark suitability, defensive chemistry, or other traits relevant to larval establishment and feeding. Similar phylogenetically structured susceptibility patterns have been documented in other woody plant–insect systems, where closely related hosts often share defensive or morphological characteristics that affect herbivore performance (Pearse & Hipp 2009, Weiblen et al. 2006).

Host age positively influenced *E. formosana* infestation severity, consistent with previous work demonstrating that older woody plants often accumulate bark fissures, wounds, or structural complexity favorable to bark-boring and cambial-feeding insects (Waring & O'Hara 2005), with *E. formosana* in particular being attracted to wounds, bark fissures, and graft unions (Winfield 1964). However, the significant interaction between origin and age indicates that age-related susceptibility varies among geographic lineages. In particular, the weaker age effect observed in Southeast Asian taxa suggests that susceptibility in these taxa may already be elevated at younger ages or may depend more strongly on climatic conditions than age factors.

The marginal effect of cultivar status suggests that cultivated varieties may differ somewhat in susceptibility, although these effects were weaker than those associated with subgenus or

geographic origin. Additional analyses incorporating cultivar-specific traits, bark morphology, or horticultural history may clarify these relationships.

The unusually large standard errors associated with several coefficients, particularly subgenera and some origin categories, indicate sparse sampling or quasi-complete separation within portions of the dataset. In regards to subgeneric differentiation in *E. formosana* severity, the divergence was primarily driven by the distinction between *Cerasus* and *Prunus*. The large odds ratio and standard error for the *Cerasus* - *Padus* comparison likely reflects sparse data within the *Padus* category, resulting in unstable parameter estimates, as all the trees that were classified under subgenus *Padus* were rated as low severity. Additional sampling across taxa within each subgenus, especially increased *Padus* sampling, would help clarify whether the detected difference between *Cerasus* and *Prunus* represents a robust phylogenetic signal in the *E. formosana* response. While these estimates should be interpreted cautiously, the broader patterns in the model remain robust and biologically consistent.

Collectively, these findings indicate that *E. formosana* infestation severity is jointly determined by host evolutionary history, host age, and climatic conditions. The interaction between phylogenetic and environmental factors suggests that future shifts in climate may alter host susceptibility patterns across ornamental and natural *Prunus* populations. Additional work integrating host chemistry, bark traits, and insect performance metrics would help clarify the mechanistic basis underlying differential susceptibility among host taxa.

Severity of Monilinia spp. brown rot

The stepwise regression approach for the abiotic variables removed minimum January temperature, frequency of precipitation in February and frequency of precipitation in April. The

stepwise regression approach for the biotic variables removed the interactions of subgenus × cultivar status, subgenus × age, and subgenus × geographic origin. The final model yielded a minimized AIC of 1745.9 (Residual Deviance: 1711.9 on 1395 degrees of freedom), down from a Null Deviance of 1957.4 on 1411 degrees of freedom, validating the final model for predicting severity of *Monilinia* spp. brown rot.

The results of the Type III analysis of deviance analysis of the final *Monilinia* spp. brown rot severity model is presented in Table 2A. Relationships between continuous abiotic and biotic predictor variables, and the probability of high severity of *Monilinia* spp. brown rot is presented in Table 2-4. The probability of high brown rot severity was significantly influenced by several taxonomic, geographic, demographic, and climatic variables. Subgenus had a strong effect on brown rot severity (LR $\chi^2 = 16.744$, $df = 2$, $p < 0.001$) (Figure 2A), indicating that susceptibility differed among major evolutionary lineages. The cultivar/species designation was also significant (LR $\chi^2 = 9.897$, $df = 1$, $p = 0.002$) (Figure 2C), suggesting that this variable contributed meaningfully to variation in disease response. Geographic origin exerted a particularly strong effect on disease severity (LR $\chi^2 = 49.996$, $df = 4$, $p < 0.001$) (Figure 2B), and age was likewise highly significant (LR $\chi^2 = 31.424$, $df = 1$, $p < 0.001$) (Figure 5A). In addition, the interaction between origin and age was highly significant (LR $\chi^2 = 87.064$, $df = 4$, $p < 0.001$), demonstrating that the influence of age on disease susceptibility varied substantially among geographic origins.

Among climatic predictor variables, maximum July temperature significantly negatively affected the probability of high brown rot severity (LR $\chi^2 = 12.459$, $df = 1$, $p < 0.001$) (Figure 5B), whereas average February temperature, average March temperature, and frequency of precipitation in March were not significant predictors (all $p > 0.05$). The model also produced

repeated warnings indicating potential quasi-complete separation within portions of the dataset, where some predictor combinations strongly or perfectly predicted disease outcome. Like the analysis on *E. formosana* severity, this was likely due to the low representation of low disease ratings within the subgenus *Padus*, and Eastern North America within the origin analysis.

Post hoc comparisons for subgenus (Table 2B, Figure 2A) revealed that the overall subgenus effect was primarily driven by a significant difference between *Cerasus* and *Prunus* (odds ratio = 0.435, $p < 0.001$), indicating substantially lower odds of high disease in *Cerasus* relative to *Prunus*. In contrast, the comparison between *Cerasus* and *Padus* was not significant ($p = 0.658$), nor was the comparison between *Padus* and *Prunus* ($p = 0.099$), although the latter showed a moderate, non-significant trend toward lower disease in *Padus*.

Post hoc comparisons among geographic origins (Table 2C, Figure 2B) showed strong regional structuring of disease risk. East Asian taxa exhibited significantly higher odds of severe disease compared to Southeast East Asian taxa (odds ratio = 11, $p = 0.002$) and similarly, species from Japan exhibited greater odds of high disease risk relative to Southeast Asian species (odds ratio = 15, $p < 0.001$). No other pairwise contrasts were statistically significant following Tukey adjustment, although comparisons involving Southeast Asia and Western Eurasia approached significance ($p = 0.072$), suggesting a possible gradient in susceptibility across regions.

The significant effect of subgenus on brown rot severity suggests that susceptibility to this disease may be partially conserved across evolutionary lineages, reflecting phylogenetically structured differences in host resistance, physiology, or pathogen interactions. Post hoc results refine this interpretation by showing that this signal is primarily driven by differences between *Cerasus* and *Prunus*, while *Padus* does not differ significantly from either group. This pattern shows that brown rot susceptibility is not uniformly distributed across subgenera but instead is

concentrated in specific evolutionary groups, potentially reflecting variation in fruit traits, phenology, or defensive chemistry that influences pathogen success (Mustafa et al. 2021).

Geographic origin emerged as one of the strongest predictors of disease severity, implying that regional evolutionary histories or local environmental adaptation may substantially influence susceptibility to cherry brown rot. The post hoc comparisons further indicate that Southeast Asian taxa are consistently more susceptible than East Asian and Japanese taxa, suggesting strong regional differentiation in host–pathogen dynamics. These differences may reflect historical variation in pathogen pressure, climatic adaptation, or trade-offs associated with growth strategies under warm, humid environments conducive to fungal disease. Although some comparisons involving Western Eurasia were not statistically significant, the overall pattern suggests a geographically structured gradient in disease risk.

The significant origin × age interaction indicates that disease susceptibility changes with age in ways that depend on geographic background. This suggests that ontogenetic trajectories of resistance are not uniform across populations, potentially reflecting differences in developmental timing, resource allocation strategies, or age-related changes in tissue susceptibility. Such context dependence reinforces the idea that disease outcomes are shaped by interacting demographic and biogeographic processes rather than single-factor effects.

Among climatic variables, maximum July temperature was the only significant predictor, suggesting that warm summer conditions play an important role in determining brown rot severity. The strong, negative correlation between late-summer heat and cherry brown rot severity highlights a vital climatic mechanism that limits disease progression in *Prunus* species. Intense summer heat desiccates active wood cankers, suppressing secondary spore production (conidia) and breaking the infection chain before fruit ripening (Lalanchette et al. 2025). While

M. fructicola and *M. laxa* are robust pathogens, their optimal metabolic growth and conidial germination occur in mild, temperate windows between 20°C and 25°C (Tamm & Flückiger 1993). When mid-summer environmental thresholds regularly exceed 30°C to 35°C, the pathogen suffers physiological heat stress. This thermal inhibition halts active mycelial expansion within the host tissue (Burnat et al. 2017). Furthermore, extreme summer heat accelerates canopy evapotranspiration, rapidly eliminating the free surface moisture and high relative humidity (>80%) that *Monilinia* conidia require to germinate and successfully penetrate plant tissues (Xu et al. 2001).

In contrast, late-winter and early-spring temperatures showed no detectable effect, indicating that preseason climatic conditions are less influential than growing-season heat in shaping disease outcomes. This contrasts with many phenological traits that are strongly regulated by spring temperatures, highlighting that pathogen-driven traits may respond more strongly to peak seasonal stress rather than transitional seasonal cues.

Finally, the presence of warnings when fitting the regression model suggests quasi-complete separation in parts of the dataset. While this may reflect biologically strong associations between certain predictor combinations and disease outcomes, it also indicates potential limitations in model stability due to sparse sampling or highly predictive factor levels. Consequently, while the results provide strong evidence for phylogenetic, geographic, and climatic structuring of brown rot susceptibility, effect sizes should be interpreted cautiously, and further sampling across taxa and regions would help confirm the robustness of these patterns.

Drivers of Tree Condition

The stepwise regression approach for the abiotic variables removed maximum July temperature, frequency of precipitation in February and March, average temperature in February, March, and April temperature. The stepwise regression approach for the biotic variables removed the interactions of subgenus × cultivar status, subgenus × age, and subgenus × origin. The final model yielded a minimized AIC of 1666.8 (Residual Deviance: 1622.8 on 1390 degrees of freedom), down from a Null Deviance of 1935.5 on 1411 degrees of freedom. However, the full model could not be reliably evaluated using Type III analysis of deviance because several interaction terms were completely aliased, indicating perfect linear dependence among predictors. Alias diagnostics revealed that multiple subgenus × origin and cultivar/species status × origin combinations were non-estimable due to sparse or absent observations within specific factor-level combinations. This lack of estimability caused the Type III analysis of deviance for the model to fail because the model could not partition variation independently among all specified effects. Because Type III tests require estimable parameters for all terms in the model, the presence of complete aliasing prevented calculation of valid likelihood-ratio statistics for the full model. The offending interaction effects (subgenus × origin and cultivar status × origin) were therefore removed from the final model.

The results of the Type III analysis of deviance analysis of the final model predicting tree condition is presented in Table 3A. The significant effect of subgenus on tree condition suggests that susceptibility or expression of the condition is at least partially structured by phylogenetic history. Differences among evolutionary lineages may reflect conserved variation in physiology, morphology, phenology, or defense-related traits that influence disease development, insect feeding tolerance/defense or stress tolerance. The strong effect of cultivar status further indicates

that variation also occurs at finer taxonomic or classification levels beyond broad subgeneric divisions, suggesting that lineage-specific responses may operate across multiple hierarchical scales.

Geographic origin was among the strongest predictors of tree condition, implying that regional evolutionary history and environmental adaptation strongly influence tree condition. Populations from different geographic regions likely experience distinct climatic regimes, pathogen communities, and selective pressures, all of which can shape resistance or susceptibility patterns. The highly significant origin × age interaction further demonstrates that age-related changes in tree condition severity differ among origins, indicating that demographic effects are context dependent rather than uniform across populations. This interaction may reflect regional differences in developmental timing, allocation strategies, structural defenses, or cumulative environmental exposure over time.

Climatic effects in the model suggest that seasonal environmental conditions also contribute to variation in tree condition. Frequency of precipitation in April significantly affected tree condition, indicating that moisture availability during early spring may influence disease development or physiological performance, leading to a tree condition rating of poor or fair. Increased April precipitation may promote pathogen establishment and spread by creating favorable conditions for fungal growth, spore dispersal, and/or prolonged tissue wetness, while also influencing host growth and tissue susceptibility during the onset of active development. These results suggest that early-season moisture conditions play an important role in shaping overall condition. Minimum January temperature exhibited only a marginal effect, suggesting that winter cold may contribute to variation in condition severity but is likely less influential than other demographic or regional factors.

Overall, the model indicates that tree condition is shaped by an interacting combination of phylogenetic structure, geographic differentiation, age effects, and seasonal climate. The particularly strong influence of geographic origin and the origin × age interaction suggests that regional adaptation and developmental context are major determinants of overall tree condition. These findings support the interpretation that responses are not controlled by a single climatic or taxonomic factor alone, but instead emerge from complex interactions among evolutionary history, local environment, and plant age.

A binomial logistic regression was used to evaluate the effects of *Monilinia* brown rot severity, *E. formosana* severity, and their interaction on tree condition. *Monilinia* brown rot severity was strongly associated with poor tree condition (LR $\chi^2 = 551.52$, df = 1, $p < 0.001$), while *E. formosana* severity also had a significant effect (LR $\chi^2 = 121.71$, df = 1, $p < 0.001$). *Monilinia* brown rot severity explained substantially more variation in tree condition than *E. formosana* severity, suggesting that disease severity was the primary factor associated with declining tree health. A significant interaction between brown rot severity and *E. formosana* severity was also detected (LR $\chi^2 = 10.24$, df = 1, $p = 0.001$). The negative interaction coefficient indicated that the combined effect of severe disease and severe insect infestation on poor tree condition was less than expected under a multiplicative model. Predicted probabilities of poor condition were approximately 13% for trees with low disease and low *E. formosana* severity, 85% for trees with high disease severity alone, 56% for trees with high infestation severity alone, and 94% for trees with both high disease and high *E. formosana* severity. Together, these results indicate that both brown rot and *E. formosana* infestation contribute to declining tree condition, although brown rot severity appears to be the dominant driver of poor condition. Additionally, *Monilinia* brown rot

exhibits highly noticeable symptoms, while the effects of *E. formosana* infestation may not be outwardly noticeable until enough of the cambium layer is consumed to girdle the tree.

Conclusions

Across the analyses of *E. formosana*, *Monilinia* spp. brown rot, and overall tree condition, results consistently demonstrate that host responses are structured by interacting effects of phylogenetic lineage, geographic origin, plant age, and seasonal climate. In all models, subgenus and geographic origin were significant predictors, indicating that evolutionary history and regional adaptation strongly shape susceptibility and condition outcomes. Age was also consistently important, and in both the brown rot and tree condition models, significant origin × age interactions showed that demographic effects vary depending on geographic background.

The *E. formosana* model was most strongly associated with spring temperature conditions, particularly February and March temperatures, suggesting that late-winter and early-spring weather play a key role in influencing tree susceptibility and/or insect development. In contrast, cherry brown rot severity was most strongly associated with summer heat, particularly maximum July temperature, indicating that growing-season conditions are more important for disease expression in this system. The tree condition model was also different, with April precipitation emerging as a significant predictor, highlighting the importance of moisture availability during early spring. Together, these results suggest that different biological processes (insect damage, fungal disease, and overall tree condition) respond to distinct seasonal weather drivers.

Post hoc analyses further refined these patterns by identifying specific phylogenetic and geographic contrasts. For *E. formosana*, differences were primarily driven by *Cerasus* vs. *Prunus*. In brown rot, *Prunus* showed higher disease odds than *Cerasus*, and Southeast Asian

taxa showed markedly higher susceptibility compared to East Asian and Japanese groups. These patterns collectively indicate that both deep evolutionary structure and regional adaptation contribute to observed variation in host response.

Limitations/future ideas

Several analytical limitations should be considered when interpreting these results. Across models, warnings of fitted probabilities approaching 0 or 1 and aliasing in interaction terms indicated quasi-complete separation and unbalanced sampling among certain taxonomic and geographic combinations. This suggests that some predictor levels were sparsely represented or absent, which can inflate effect sizes and reduce the stability of coefficient estimates. In particular, interaction terms involving subgenus and origin were sensitive to uneven sampling structure.

Future work should prioritize improving sampling balance across subgenus × origin combinations and across age classes to reduce structural sparsity. Expanding geographic representation within each taxonomic group would also help disentangle phylogenetic versus environmental effects. Specifically, subgenus *Padus* and trees originating from Eastern North America were under-represented. Methodologically, alternative approaches such as penalized logistic regression (e.g., Firth correction) or Bayesian hierarchical models could improve parameter stability under separation and better accommodate uneven sampling designs. Incorporating finer-scale data and host trait measurements (e.g., phenology, tissue chemistry, etc.) would also help clarify mechanisms underlying observed patterns.

Broader management implications

These results suggest that risk of insect damage, disease severity, and overall tree condition in *Prunus* spp. is not uniform across taxa or regions but is instead strongly structured by both evolutionary lineage and environmental context. From a management perspective, this implies that susceptibility screening and monitoring programs should account for both species' identity and geographic origin, rather than treating host populations as ecologically equivalent.

The strong climatic signals across models also indicate that different stressors are driven by different seasonal windows. *Enarmonia formosana* risk appears most sensitive to late-winter and early-spring temperatures, brown rot risk to summer heat conditions, and tree condition to early-spring precipitation. This suggests that predictive management tools could be improved by incorporating season-specific weather metrics rather than relying on annual averages. For example, early-season monitoring may be particularly important for anticipating severity of *E. formosana*, while mid-summer conditions may better predict brown rot risk.

Finally, the consistent importance of origin × age interactions highlights that susceptibility changes over time in a region-dependent manner. This suggests that management strategies may need to be tailored not only to species or site conditions but also to stand age structure and regional provenance. Overall, integrating phylogenetic information with seasonal climate forecasting could improve risk prediction and inform more targeted, temporally specific disease and pest management strategies.

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Tables

Table 2-1: A, B, and C: (A) Type III analysis of deviance for factors associated with *Enarmonia formosana* severity ratings. Text in bold indicates significant predictor variables. (B) Tukey-adjusted pairwise comparison of estimated marginal means (EMMs) among sub subgenera (*Cerasus*, *Prunus*, and *Padus*) (C) Tukey-adjusted pairwise comparison of estimated marginal means (EMMs) among geographic origins (East Asia, Eastern North America, Japan, Southeast Asia, and Western Eurasia). All post hoc tests were performed on the log odds ratio scale and results are presented as odds ratios. All comparisons report df = Inf, which is typical for post hoc tests derived from generalized linear mixed models. This means p-values are based on normal (z) approximations rather than chi-square distribution.

A

Predictor	LR χ^2	df	P-value
Average March temperature	**32.157**	**1**	**<0.001**
origin:age	**15.301**	**4**	**0.00412**
Average February temperature	**13.207**	**1**	**<0.001**
subgenus	**10.211**	**2**	**0.00606**
Geographic Origin	**9.99**	**4**	**0.0406**
Tree age	**9.031**	**1**	**0.00265**
Maximum July temperature	**5.707**	**1**	**0.0169**
Cultivar/species status	3.733	1	0.0533
Frequency of precipitation in March	2.88	1	0.0897

B

Contrast	Odds ratio	SE	z-ratio	p-value
Cerasus / Padus	3.52×10^6	2.33×10^9	0.023	0.999
Cerasus / Prunus	**2**	**0**	**2.423**	**0.041**
Padus / Prunus	0	0	-0.022	0.999

C

Contrast	Odds ratio	SE	z-ratio	p-value
E Asia / E NA	1.566	1260	0.001	1
E Asia / Japan	**0.534**	**0.082**	**-4.101**	**<0.001**
E Asia / SE Asia	8.509	7.52	2.422	0.109
E Asia / W Eurasia	2.98	1.86	1.753	0.402
E NA / Japan	0.341	274	-0.001	1
E NA / SE Asia	5.434	4360	0.002	1
E NA / W Eurasia	1.903	1530	0.001	1
Japan / SE Asia	**15.938**	**14**	**3.161**	**0.014**
Japan / W Eurasia	**5.582**	**3.44**	**2.786**	**0.043**
SE Asia / W Eurasia	0.35	0.373	-0.985	0.862

Table 2-2: A, B, and C: (A) Type III analysis of deviance for factors associated with *Monilinia* spp. brown rot severity ratings. Text in bold indicates significant predictor variables. (B) Tukey-adjusted pairwise comparison of estimated marginal means (EMMs) among subgenera (*Cerasus*, *Prunus*, and *Padus*) (C) Tukey-adjusted pairwise comparison of estimated marginal means (EMMs) among geographic origins (East Asia, Eastern North America, Japan, Southeast Asia, and Western Eurasia). All post hoc tests were performed on the log odds ratio scale and results are presented as odds ratios. All comparisons report df = Inf, which is typical for post hoc tests derived from generalized linear mixed models. This means p-values are based on normal (z) approximations rather than chi-square distribution. Several comparisons produced extremely large or zero odds ratios due to quasi-complete separation in the data. These estimates are not interpretable as effect sizes and are reported as NA.

A

Predictor	LR χ^2	df	P-value
origin:age	**87.064**	**4**	**<0.001**
Geographic Origin	**49.996**	**4**	**<0.001**
Tree age	**31.424**	**1**	**<0.001**
subgenus	**16.744**	**2**	**<0.001**
Maximum July temperature	**12.459**	**1**	**<0.001**
Cultivar/species status	**9.897**	**1**	**0.002**
Frequency of precipitation in March	2.059	1	0.151
Average March temperature	0.481	1	0.488
Average February temperature	0.051	1	0.821

B

Contrast	Odds ratio	SE	z-ratio	p-value
Cerasus / Padus	1.838	1.28	0.872	0.658
Cerasus / Prunus	**0.435**	**0.0967**	**-3.744**	**<0.001**
Padus / Prunus	0.237	0.166	-2.058	0.099

C

Contrast	Odds ratio	SE	z-ratio	p-value
E Asia / E NA	NA (inflated)	NA	0.035	1
E Asia / Japan	1	0	-1.975	0.279
E Asia / SE Asia	**11**	**7**	**3.711**	**0.002**
E Asia / W Eurasia	2	1	1.405	0.6242
E NA / Japan	NA (zero estimate)	NA	-0.035	1
E NA / SE Asia	NA (zero estimate)	NA	-0.034	1
E NA / W Eurasia	NA (zero estimate)	NA	-0.035	1
Japan / SE Asia	**15**	**9**	**4.189**	**< 0.001**
Japan / W Eurasia	2	1	2.153	0.198
SE Asia / W Eurasia	NA (zero estimate)	NA	-2.593	0.072

Table 2-3: A, B, and C: (A) Type III analysis of deviance for factors associated with tree condition ratings. Text in bold indicates significant predictor variables. (B) Tukey-adjusted pairwise comparison of estimated marginal means (EMMs) among subgenera (*Cerasus*, *Prunus*, and *Padus*) (C) Tukey-adjusted pairwise comparison of estimated marginal means (EMMs) among geographic origins (East Asia, Eastern North America, Japan, Southeast Asia, and Western Eurasia). All post hoc tests were performed on the log odds ratio scale and results are presented as odds ratios. All comparisons report df = Inf, which is typical for post hoc tests derived from generalized linear mixed models. This means p-values are based on normal (z) approximations rather than chi-square distribution. Several comparisons produced extremely large or zero odds ratios due to quasi-complete separation in the data. These estimates are not interpretable as effect sizes and are reported as NA.

A

Predictor	LR χ^2	df	P-value
origin:age	**125.913**	**4**	**< 0.001**
Geographic Origin	**82.627**	**4**	**< 0.001**
Tree age	**52.101**	**1**	**< 0.001**
Cultivar/species status	**20.766**	**1**	**< 0.001**
subgenus	**12.363**	**2**	**0.002**
Frequency of precipitation in April	**9.244**	**1**	**0.002**
Minimum January temperature	3.114	1	0.078

B

Contrast	Odds ratio	SE	z-ratio	p-value
Cerasus / Padus	0.731	0.453	-0.506	0.868
Cerasus / Prunus	**0.449**	**0.104**	**-3.468**	**0.002**
Padus / Prunus	0.614	0.384	-0.78	0.715

C

Contrast	Odds ratio	SE	z-ratio	p-value
E Asia / E NA	NA (inflated)	NA	2.682	0.057
E Asia / Japan	1.07	0.15	0.446	0.992
E Asia / SE Asia	**15**	**9.74**	**4.187**	**< 0.001**
E Asia / W Eurasia	0.966	0.35	-0.094	1
E NA / Japan	NA (zero estimate)	NA	-2.663	0.06
E NA / SE Asia	NA (zero estimate)	NA	-1.934	0.299
E NA / W Eurasia	NA (zero estimate)	NA	-2.688	0.056
Japan / SE Asia	**14.1**	**9.01**	**4.144**	**< 0.001**
Japan / W Eurasia	0.906	0.33	-0.271	0.999
SE Asia / W Eurasia	**0.064**	**0.05**	**-3.823**	**0.001**

Table 2-4: Relationships between continuous abiotic and biotic predictor variables, and the probability of high severity of *Enarmonia formosana* and brown rot caused by *Monilinia* species. Significance of categorical predictors are indicated in Tables 2-1, 2-2, and 2-3.

Abiotic factors	Enarmonia formosana	*Monilinia* spp.
Minimum January temperature	0	*0*
Maximum July temperature	++	--
Average February temperature	++	0
Average March temperature	++	0
Average April temperature	0	0
Frequency of precipitation in February	0	0
Frequency of precipitation in March	+	0
Frequency of precipitation in April	0	0
Biotic factor		
Tree age	++	++

++ : significantly positive (P<0.05)
+ : non-significant positive trend (0.05<P<0.1)
0 : no effects
- : non-significant negative trend (0.05<P<0.1)
-- : significantly negative (P<0.05)

Figures

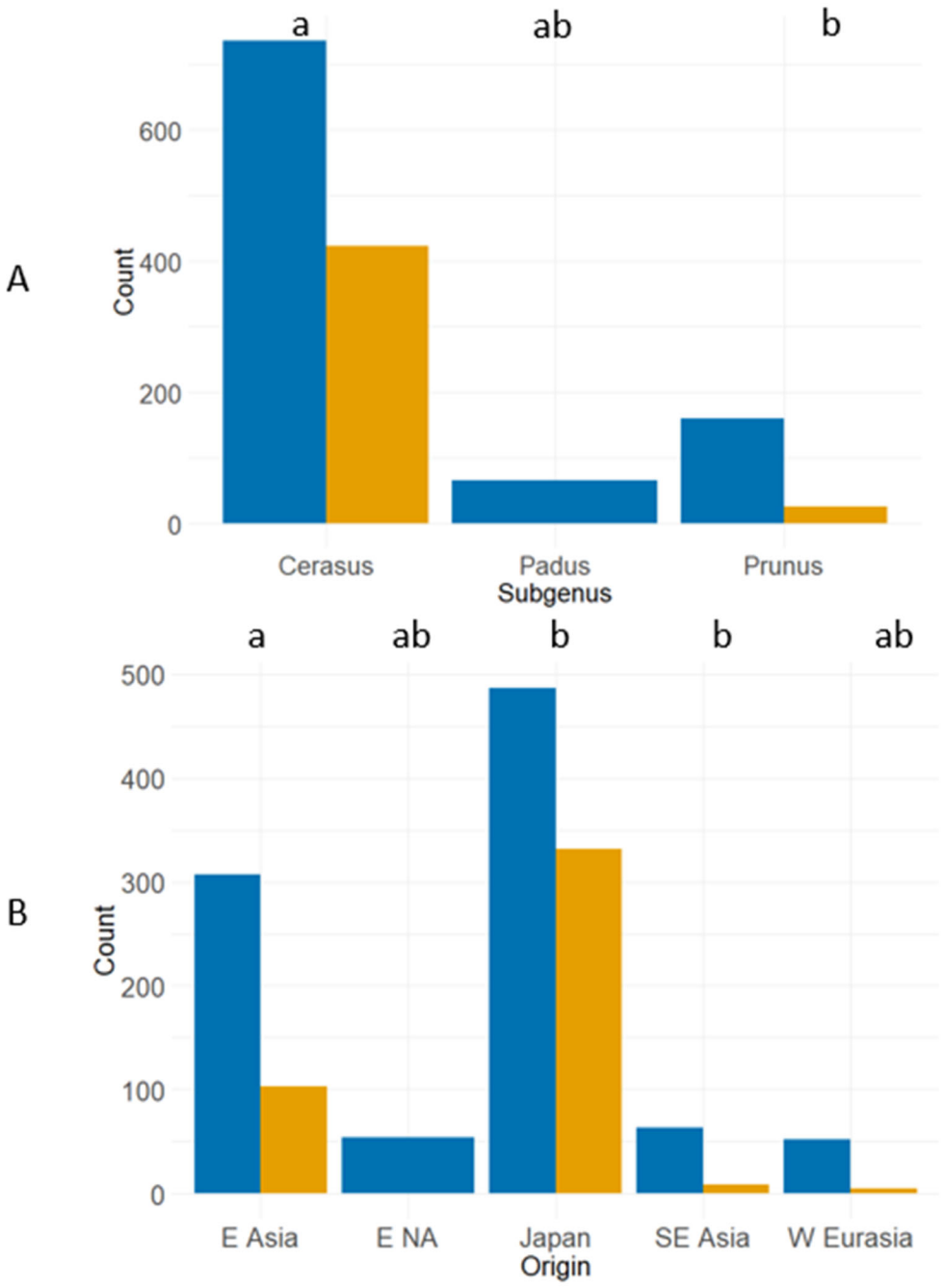

Figure 2-1: A and B: Counts of *Enarmonia formosana* by rating; blue bars are low severity ratings, and orange bars are high severity ratings. Lowercase letters above the bars represent statistically similar groups. (A) Ratings by subgenus. (B) Ratings by geographic origin.

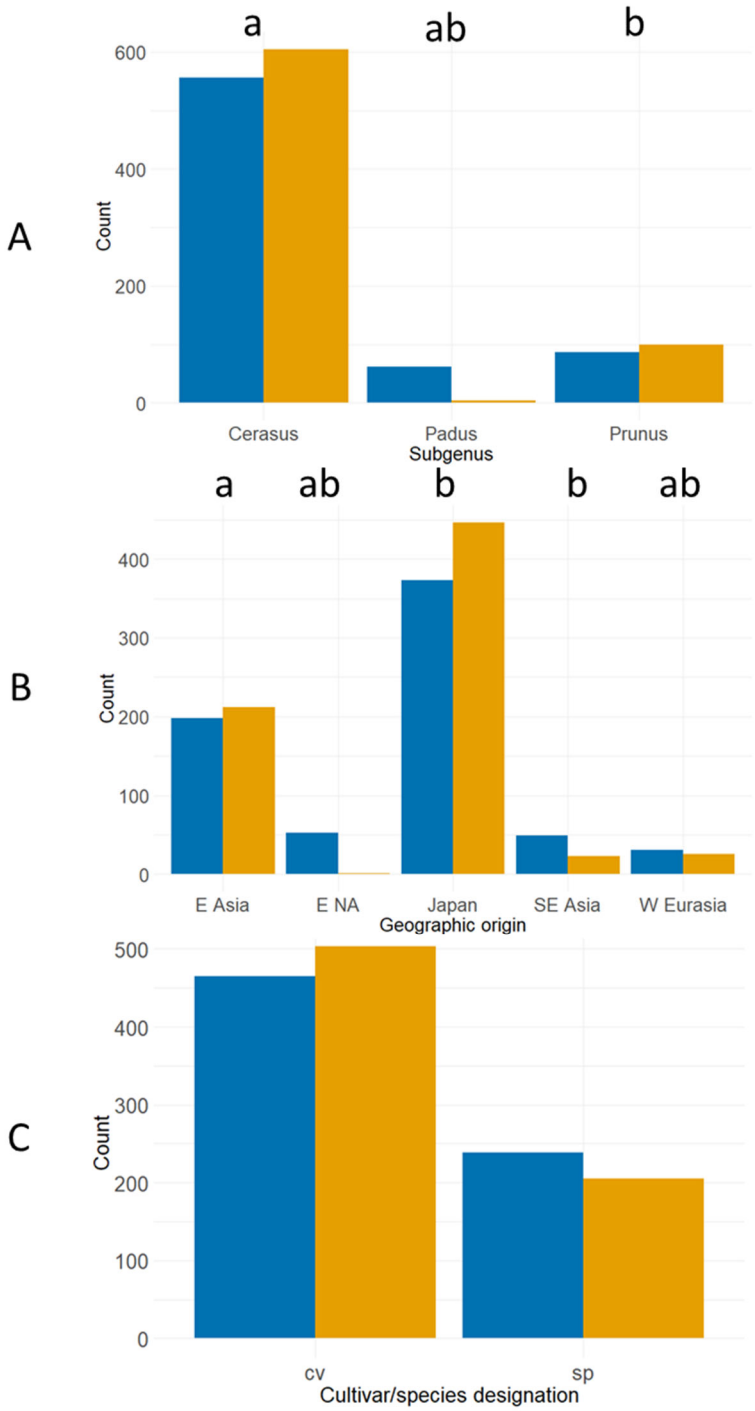

Figure 2-2: A, B, and C: Counts of *Monilinia* spp. brown rot ratings by rating; blue bars are low severity ratings, and orange bars are high severity ratings. Lowercase letters above the bars represent statistically similar groups. (A) Ratings by subgenus. (B) Ratings by geographic origin. (C) Ratings by cultivar/species designation.

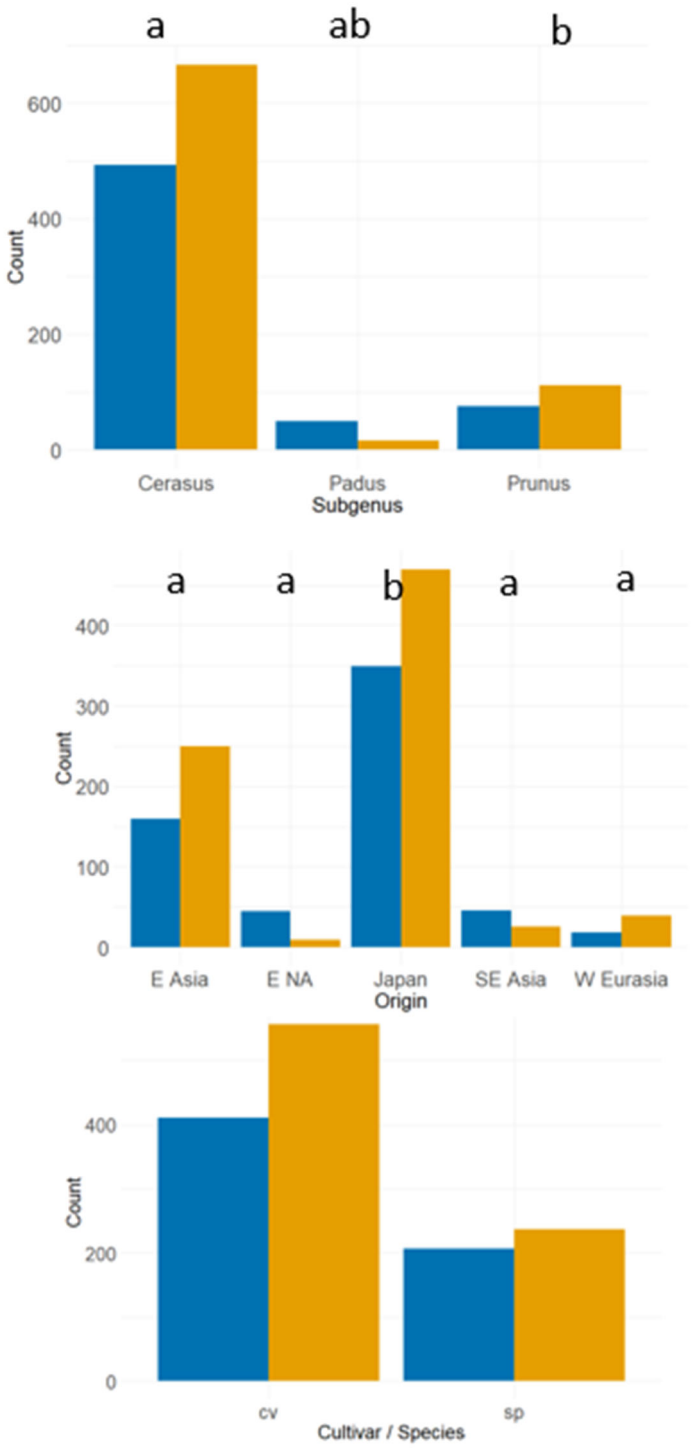

Figure 2-3: A, B, and C: Counts of tree condition by rating; blue bars are low severity ratings, and orange bars are high severity ratings. Lowercase letters above the bars represent statistically similar groups. (A) Ratings by subgenus. (B) Ratings by geographic origin. (C) Ratings by cultivar/species.

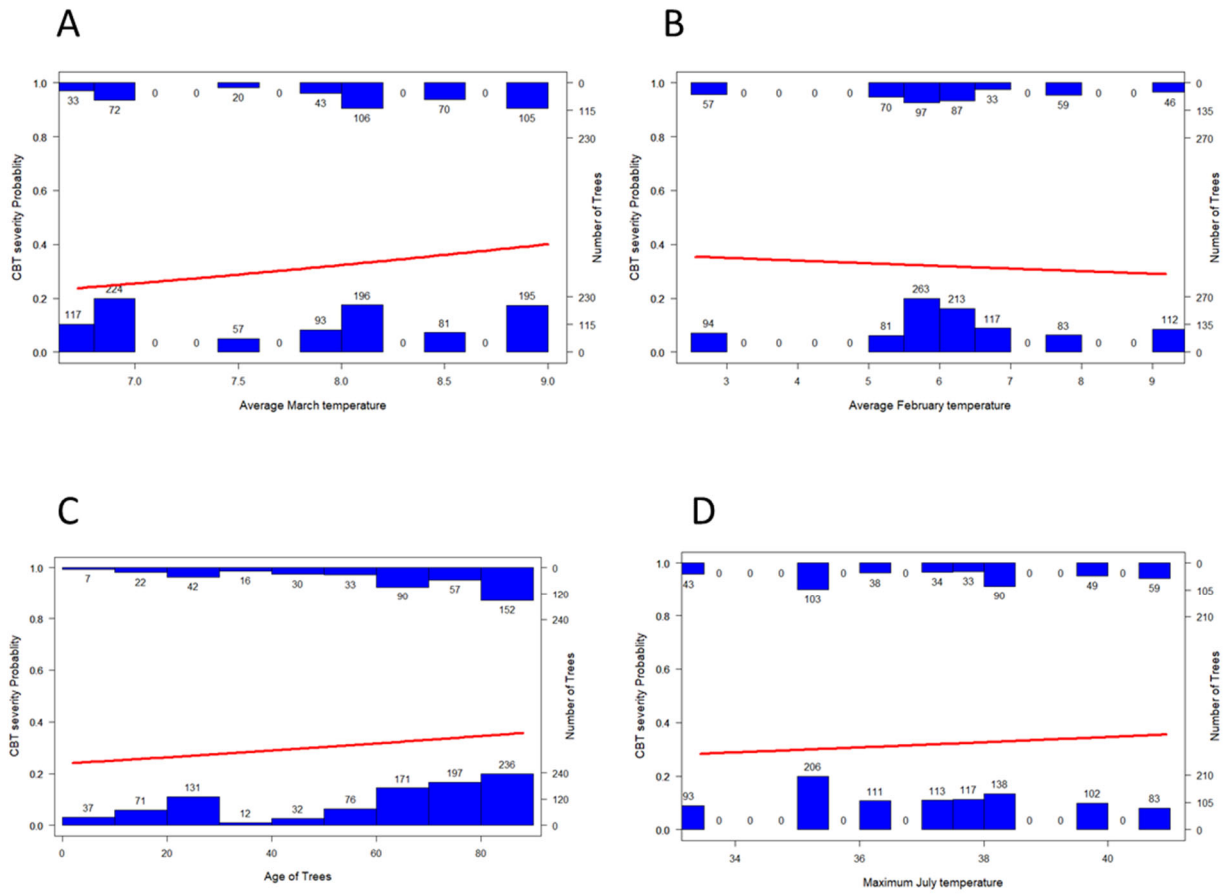

Figure 2-4: A, B, C, and D: Logistic regression of the probability of *Enarmonia formosana* high severity by (A) average March temperature. (B) average February temperature. (C) tree age. (D) Maximum July temperature. All predictor variables shown were significant in the final full model ($p < 0.05$).

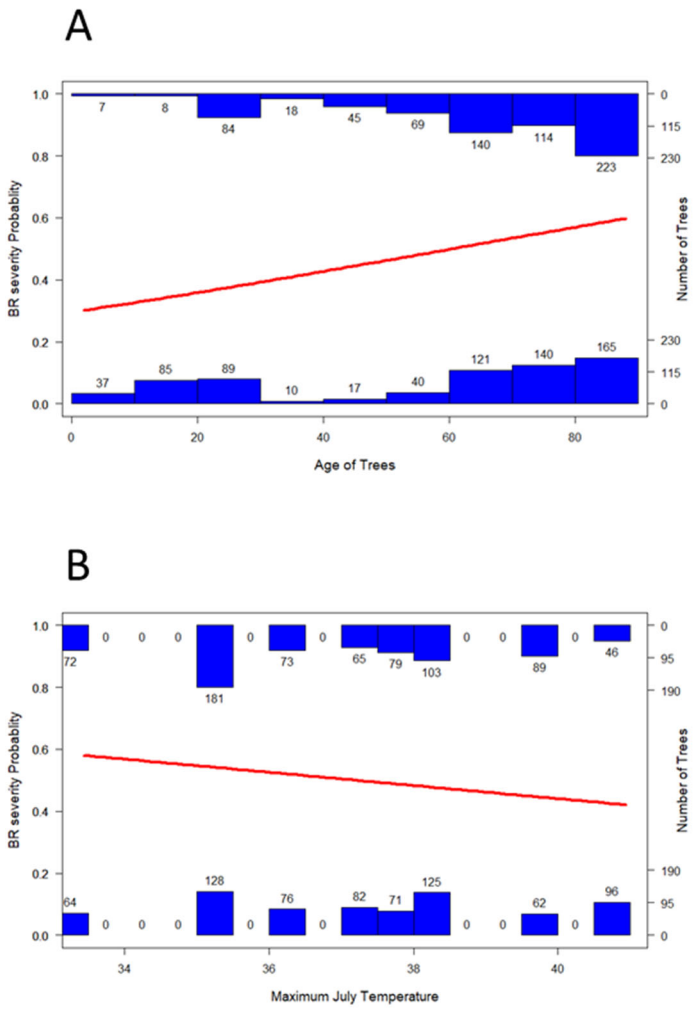

Figure 2-5: A and B: Logistic regression of the probability of *Monilinia* spp. brown rot high severity by (A) tree age. (B) maximum July temperature. Both predictor variables shown were significant in the final full model ($p < 0.05$).

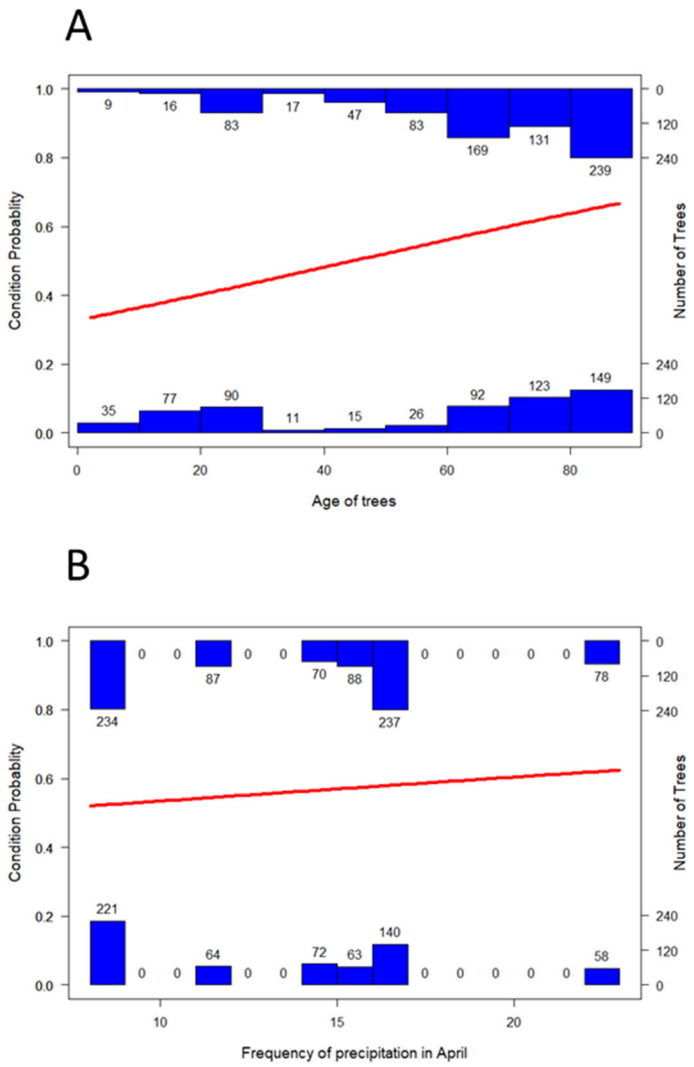

Figure 2-6: A and B: Logistic regression of the probability of poor/fair tree condition by (A) tree age. (B) frequency of precipitation in April. Both predictor variables shown were significant in the final full model ($p < 0.05$).

Chapter 3 Predicting invasive Asian high-impact insect herbivores to Pacific Northwest forest trees using host evolutionary history

Abstract

Insects play important roles in food web interactions as herbivores, saprophages, predators, and parasites, as well as in ecosystem processes such as pollination, biogeochemical cycling, and ecological succession. Given their species richness, global distribution, and roles in ecosystem processes, it is not surprising that insects are also dominant as non-native species both in terms of their number and their impacts. Most non-native insect invaders do not cause much damage, but a few of these cause profound ecological and economic impacts. Unfortunately, there tend to be limited resources to detect arriving insects, and only a fraction of incoming cargo and baggage is inspected. Furthermore, after an invasive insect herbivore successfully establishes and begins to spread, eradication becomes increasingly infeasible. Establishing management priorities can also be challenging in an ever-changing global trade landscape. Therefore, prediction and prevention remain an important approach in addressing invasive insect species.

In this chapter, I conducted a literature review and extended previous published models to predict the potential impact of herbivorous insects native to east Asia, but not yet established in North America, in Pacific Northwestern woody plants. The Pacific Northwest and east Asia share a complex geological and biological history, and the Pacific Northwest also harbors the world's largest remaining extents of temperate rainforests, representing an ecologically unique ecosystem with high biodiversity importance. Potential invasive insect species were identified through a comprehensive review of east Asian forest insect literature. Species were verified as native to east Asia using occurrence records and host plant associations, and feeding guilds were

determined through literature review. I also compiled a dataset of native North American congener insects associated with regional tree species; these insects could provide biotic resistance to introduced species from Asia, especially on shared hosts. Phylogenetic divergence times between Asian host plants and their Pacific Northwest congeners was used as the primary metric of invasion risk based upon previously published models. Asian insects were then rated as a low, moderate, or high risk of having a high impact based upon the estimated phylogenetic distance between their evolutionarily-native host in Asia and its congener host plant in North America. High impact was defined as those species that can cause population-level mortality in their host plants.

The results highlight how evolutionary relatedness provides a useful framework for anticipating novel host associations prior to the introduction of a non-native herbivorous insect. Shared ancestry between east Asian and Pacific Northwestern temperate floras likely increase susceptibility to host shifts because many genera could retain conserved structural and chemical characteristics despite geographic separation. These findings support previous biogeographic and ecological work emphasizing the strong floristic affinity between the temperate forests of eastern Asia and western North America. The study further highlights the vulnerability of ecologically significant Pacific Northwestern forest ecosystems, including riparian forests and Garry oak ecosystems, where invasive herbivores could alter nutrient cycling, regeneration dynamics, and biodiversity.

Introduction

Insects play important roles in food web interactions as herbivores, saprophages, predators, and parasites, as well as in ecosystem processes such as pollination, biogeochemical cycling, and ecological succession (Kremen & Chaplin-Kramer 2007, Noriega et al. 2018, Schonly et al. 1991). Additionally, insects are the world's most species rich group of organisms with >1 million described species, and perhaps millions more species that remain undescribed (Gaston 1991, Groombridge and Jenkins 2002). Given their species richness, global distribution, and roles in ecosystem processes, it is not surprising that insects are also dominant as non-native species both in terms of their number and their impacts (Yamanaka et al. 2015, Brockerhoff & Liebhold 2017, Venette & Hutchinson 2021).

The most widely reported ecological and economic harm caused by non-native insects are those by plant-killing herbivores, which threaten forest ecosystems worldwide (Brockerhoff & Liebhold 2017). Forest ecosystems are of immense global importance in delivering a myriad of benefits to humanity (Bonan 2008, Schwenk et al. 2012). Most non-native insects arrive in their new locations as a result of global trade and travel, and may be transported with their hosts when plants and plant products are shipped, or in solid wood packing material (McCullough et al. 2006, Dehnen-Schmutz et al. 2007, Allen et al. 2017, Liebhold et al. 2012). Fortunately, most non-native species that arrive will not establish successfully, and those that do establish are relatively innocuous in an introduced region (Williamson & Fritter 1996, Simberloff & Gibbons 2004, Liebhold & Tobin 2008, Aukema et al. 2010). However, there are a few that can cause profound ecological and economic impacts (Bradshaw et al. 2016, Cuthbert et al. 2022). For example, several species of ash trees (*Fraxinus* spp.) are threatened with functional extinction in the United States due to the introduced Asian emerald ash borer *Agrilus planipennis* (Herms &

McCullough 2014), and the American chestnut (*Castanea dentata*) has already been rendered functionally extinct by the chestnut blight, *Cryphonectria parasitica* (Anagnostakis 1987). Unfortunately, there tend to be limited resources to detect arriving insects, and only a fraction of incoming cargo and baggage generally is inspected (Brockerhoff et al. 2006, Work et al. 2006, Turner et al. 2021). Furthermore, after an invasive insect herbivore successfully establishes and begins to spread, eradication becomes increasingly infeasible (Tobin et al. 2014). Establishing management priorities can also be challenging in an ever-changing global trade landscape. Therefore, prediction and prevention remain an important approach in addressing invasive insect species (Venette & Hutchinson 2021).

Not surprisingly, the ability to identify which non-native species will cause ecological and/or economic damage prior to their arrival in a novel range remains a central goal of invasion science (Foucaud et al. 2020). Numerous studies have addressed the reasons for successful invasion, and most attribute it to characteristics of the invaded ecosystems or to characteristics of the invader (Catford et al. 2008, Richardson & Pyšek 2006, Thuiller et al. 2005). Ecosystem and climatic similarity between the native and introduced range is necessary for successful establishment, but not predictive of invasiveness. Also, some invader traits are predictive in some situations, but still tend to be poor predictors of invasiveness and impact (Kolar & Lodge 2001, Mech et al. 2019).

In a native range, insects evolve with their host plants and natural enemy communities, which provide important bottom-up and top-down control, respectively. However, these constraints are released when an insect is introduced into a novel range. Consequently, the defense-free space hypothesis (Desurmont et al. 2011, Showalter et al. 2018) and the enemy release hypothesis (Keane & Crawley 2002, Liu & Stiling 2006) have been proposed to partially explain why some

introduced species become highly invasive in a new region. Recent studies have pinpointed the specific importance of evolutionary history of introduced insect herbivores and their host plants as robust predictors of high-impact insect invasions in which tree mortality occurs across a population of relatively healthy host trees (Mech et al. 2019, Schulz et al. 2021, Uden et al. 2022, Schulz et al. 2025). These studies have demonstrated that high impacts of a non-native insect herbivore depend mostly on how closely related plant hosts in the introduced range are to those in the insect's native range. Specifically, divergence times between hosts in the native and introduced ranges of a non-native insect can be used to predict the potential for high impacts caused by the insect. Another finding of these studies is that in some cases, the presence of a North American congener insect species on a shared plant host decreases the probability of high impact in the introduced insect species, presumably due to biotic resistance from competition or natural enemies of the North American congener insect species. These models have been shown to be relatively stable when applied to coniferous or deciduous hosts (Mech et al. 2019, Schulz et al. 2021, Schulz et al. 2025). This work also provided a framework to predict high impact in European species of insects not yet established in North America and quantify the vulnerability of host trees native to North America if establishment were to occur (Uden et al. 2022).

In this chapter, my objective is to predict the potential impact of insects native to east Asia, but not yet established in North America, in Pacific Northwestern woody plants. The Pacific Northwest and east Asia share a complex geological and biological history. Tectonic movements and sea level changes due to climatic shifts separated and periodically reattached these continents, allowing the repeated transfer of plant and animal populations (Hopkins 1959). About 20,000 years ago, when the world climate system moved from a glacial state into the present interglaciation known as the Holocene (Hopkins 1959), the vast continental ice sheets

disappeared, sea levels rose worldwide, land and ocean surfaces warmed, and moisture became redistributed (Jacobson et al. 1987, Whitlock 1992). In the Pacific Northwest, the retreat of glacial ice revealed a landscape of glacial meltwater debris in the lowlands, and this region was colonized by the biota that survived in the unglaciated region to the south, along the exposed coastal shelf, and in the highlands (Whitlock 1992). This colonization eventually developed into the conifer dominated forests, unique among the temperate forests of the world, on the slopes of the Cascade and Coastal ranges of Oregon, Washington, northern California, and British Columbia (Franklin & Waring 1979). They are well known for old growth stands dominated by Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) (Franklin & Waring 1979).

The Pacific Northwest also harbors the world's largest remaining extents of temperate rainforests and represents an ecologically unique ecosystem with high biodiversity importance (Brandt et al. 2014, DellaSala 2011). For these reasons it is particularly important to identify potential threats from insect herbivores that may cause high impacts in Pacific Northwestern forests. Based on the role of evolutionary history between host trees in the native and introduced range in driving invasive insect impact (e.g., Mech et al. 2019, Schulz et al. 2021, Schulz et al. 2025), it is likely that many insect threats to Pacific Northwestern forests are insects native to east Asia. Due to the importance of climate suitability in non-native insect establishment (Hulme 2017, Venette 2017), I focused on a geographic area of Asia that contained temperate forests with roughly the same climate as the Pacific Northwest; this area included China, Japan, Korea, Russian Far East, Taiwan, and Vietnam.

Materials and Methods

Study area

In North America the study focused on temperate forested areas of the Pacific Northwest, which occupy a broad coastal and montane region along the western margin of the continent, extending from northern California through Oregon and Washington and into coastal British Columbia and southeastern Alaska.

The region of Asia considered for this study is the temperate forest zone of East Asia which forms a broad, ecologically diverse belt stretching from the Pacific coast inland to the foothills and basins surrounding the Tian Shan. This region includes much of eastern China, the Korean Peninsula, Japan, Taiwan, and portions of the Russian Far East. The forests occur where precipitation and seasonal temperatures are sufficient to support deciduous, mixed, or montane conifer forests rather than steppe, desert, or subtropical evergreen systems. Areas of southeast Asia where temperate forests occur were also considered. These are generally restricted to the mountainous areas of Vietnam, Laos, Cambodia, and Thailand, as non-mountainous areas are generally considered tropical or subtropical.

Identification of host trees

Potential host tree species of Pacific Northwestern forests were first identified from Urban et al. (1993). To focus on host trees with a higher likelihood of evolutionary history with trees native to Asia, I then selected 38 species that had an Asian congener species. This final list contained 38 species: 21 angiosperm species representing 11 genera, and 17 gymnosperm species representing 8 genera (Table 1). Asian host trees were identified by choosing genera that

matched the list of Pacific Northwest forest trees using Norman Shaw's Chinese Forest Trees and Timber Supply (1915). Additional trees were added to this list as host trees were identified from the Asian insect herbivore list. A total of 172 Asian host trees were identified, which included 112 angiosperm species representing 11 genera, and 60 gymnosperm species representing 8 genera (Table 2). All Pacific Northwestern tree genera had at least one congener Asian tree species.

Asian Insects

Insect herbivores that feed on these Asian congener host species were identified from the available literature and verified that they were not known to be established in North America; this group will constitute the list of potential insect risk species. This list was compiled using the primary reference, Forest Insects of China (Xiao 1992), a comprehensive guide detailing the biology, ecology, and management of forest insects native to China. From this list, insect orders that are known to not be phytophagous were removed (e.g., Formicidae, Mantidae). Additional insects were included from a literature review of forest insect pests in China (Ji et al. 2011), the Russian Far East (Musolin et al. 2022), Korea (Choi et al. 2019, Lee et al. 2012), and Japan (Kamata 2002).

The Global Biodiversity Information Facility database (GBIF) (GBIF 2026) was then queried to ensure each insect was indeed native to east Asia. This database has georeferenced occurrences, which was used to determine geographic origin. Additionally, this database contains common and scientific names of records, from which I compiled synonyms of all species on the insect list. The current taxonomy of all species was initially compiled using the NCBI taxonomy browser (O'Leary et al. 2024) but iNaturalist (iNaturalist 2026) and GBIF (GBIF 2026) were used if the

taxonomy was incomplete in the NCBI taxonomy browser. Order, suborder, superfamily, family, subfamily, tribe, subtribe, and genus were compiled (as available) for each insect species.

Host tree and feeding guild

A literature search was conducted to determine the host plant of each Asian insect species. A plant host was sometimes, but not always, available from the sources used to build the list (Xiao 1992, Ji et al. 2011, Musolin et al. 2022, Choi et al. 2019, Lee et al. 2012). The information in these original sources was often limited to genus, so a search was made to identify host plant to species and/or identify other plant hosts in more detailed sources.

One of six feeding guild categories was assigned to each insect species, and I used the classification from Mech et al. (2019). These guilds were folivore, wood feeding, gall-forming, reproductive plant part feeding, sap-feeding, and root-feeding. When two feeding guilds were found in the literature, the guild most associated with economic or ecological impacts was chosen. For example, larvae of *Chrysobothris igai* Latreille, are wood-feeding as they feed within the phloem, but its adults feed on leaves or pollen and cause limited damage compared to the larvae; thus, this species was classified as being in the wood feeding guild.

A list of Asian insect herbivores that feed on selected Asian forest trees (Table 2) is presented in Appendix 1. A list of sources used to determine the host tree and feeding guild for each Asian insect species is presented in Appendix 2.

North American congener insects

I compiled a list of North American insect genera associated with each Pacific Northwest American tree (Table 3), using the same protocol as Mech et al. (2019). For each tree species, seven sources were queried for insects that utilize it as a host. These sources were Silvics of North America (USDA 2025), Great Basin Naturalist Memoirs (Wood & Bright 1992), Aphids of the world database (Favret & Aphid Taxon Community 2026), HOSTS Lepidopteran database (Robinson et al. 2023), Discover Live website (Schuh et al. 2010), Western Forest Insects (Furniss et al. 2002), and Insects that Feed on Trees and Shrubs (Johnson & Lyon 1994). For each insect, I also used the GBIF database (GBIF 2026) to ensure that the species was native to the Pacific Northwest, which was especially important as many of these sources also list invasive insect species that feed on North American host plants. Feeding guild was also determined from each insect species, and taxonomic information was obtained from NCBI (O'Leary et al. 2024), iNaturalist (iNaturalist 2026), and/or GBIF (GBIF 2026).

Tree divergence time

Divergence times between insect host plants in the native (Asia) and potential introduction (Pacific Northwest) regions were estimated using TimeTree (Kumar et al. 2022). The molecular time estimates in TimeTree represent a synthesis of published time estimates that were obtained from scientific literature. A detailed description of how estimates were derived is available in Kumar et al. (2022) and Hedges et al. (2015). Pairwise divergence estimates were not available in TimeTree for *Salix* and *Populus* species. Thus, subgenus divergence time estimates were made from available phylogenetic studies (Liu et al. 2022 for *Populus*, Ogutcen et al. 2024 for *Salix*).

Divergence times between host taxa were represented as millions of years before present and used as the primary indicator of evolutionary distance among hosts.

Impact rating of Asian insects

Using the time estimates from TimeTree, a pairwise matrix of both gymnosperms and angiosperms was created, and Asian insects were assigned a rating of low, moderate, or high risk of high impact based upon the divergence time between their native Asian host and their likely North American host if introduced. High impact was defined in accordance with Mech et al. (2019) as those species that can cause population-level mortality in their host plants. For conifer specialist insect herbivores, high risk of high impact was assigned when the host-pair divergence time was 2.8-4.8 million years ago (MYA); moderate risk of high impact was assigned when the host-pair divergence time was 2 to <2.8 or >4.8 to 10 MYA; and low risk of high impact was assigned for all other divergence times (Mech et al. 2019, Uden et al. 2022). For angiosperm specialist insect herbivores, high risk of high impact was assigned when the host-pair divergence time was 4.5-6.5 MYA; moderate risk of high impact was assigned when the host-pair divergence time was 2 to <4.5 or >6.5 to 25 MYA; and low risk of high impact was assigned for all other divergence times (Schulz et al. 2021, Schulz et al. 2025). From these assignments, I then compiled a list of Asian insects and their native host, their risk rating based upon the divergence time of the host-pair, and the presence or absence of a native North American insect congener.

Results

Asian insects and North American congener insects

A total of 805 insect species associated with Chinese forests were compiled from *Forest Insects of China* (Xiao 1992). An additional 68 species were added from the regional sources (Ji et al. 2011, Musolin et al. 2022, Choi et al. 2019, Lee et al. 2012, Kamata 2002), yielding a combined dataset of 873 species. After filtering to retain only phytophagous insects whose native Asian host plant genus matched the North American host list, and excluding non-native taxa, 368 Asian phytophagous forest insect species remained. This subset, hereafter referred to as the Asian focus assemblage, is presented in Appendix 1.

The Asian focus assemblage was dominated by Lepidoptera (197 species) and Coleoptera (107 species), followed by Hemiptera (35 species), Hymenoptera (28), and Diptera was represented by a single species (Figure 1). Across feeding guilds, folivores were most abundant (248 species), followed by wood feeders (66 species) and sap feeders (36 species). Reproductive tissue feeders (10 species), root feeders (3 species), and gall formers (2 species) were comparatively fewer in number (Figure 2). From the insects contained in the Asian focus assemblage, I identified 107 native North American congener species that feed on the North American host plant list (Table 1). Of these 107 species, 50 were in Coleoptera, 38 in Hemiptera, 12 were Hymenoptera, and 7 in Lepidoptera.

Divergence matrices and host risk summary

A matrix of Pacific Northwest and Asian angiosperms with their pairwise potential impact rating is provided in Figure 4, and a matrix of Pacific Northwest and Asian gymnosperms is provided in Figure 5. A host risk summary table listing Pacific Northwest native trees and the number of risk associations is presented in Table 4. The host-risk summary table revealed substantial variation in invasion risk categories among Pacific Northwest host genera. Across angiosperms, moderate risk ratings of Asian insects that did not have a North American congener were the dominant category. *Quercus garryana* had the greatest number of moderate risk ratings (204), followed by *Alnus sinuata* (50), *Alnus rubra* (47), and *Alnus incana* ssp. *tenuifolia* (44). A notable number of moderate risk ratings also occurred in *Populus*, *Salix*, *Malus*, and *Fraxinus* (Table 4, Figure 3).

High risk ratings of Asian insects were comparatively uncommon and occurred primarily in a small number of hosts. *Betula papyrifera* was associated with five high risk ratings that lacked North American insect congeners, while *Populus balsamifera* ssp. *trichocarpa* was associated with eight such ratings. Moderate risk ratings of Asian insects for which a native North American insect congener was present were most frequent in *Quercus garryana* (10), followed by *Larix occidentalis* (9) and *Fraxinus latifolia* (5) (Table 4).

Low risk ratings were concentrated largely within gymnosperm hosts. *Pinus monticola*, *P. contorta*, and *P. ponderosa* each had 83 Asian insects with low risk rating and without a native North American congener, and 40 Asian insects with a low risk rating and with a native congener present. Similarly, *Picea sitchensis* and *Picea engelmannii* were associated primarily with Asian insects that had low risk ratings. In contrast, several angiosperm hosts, including

Prunus emarginata, *Prunus virginiana*, and *Acer macrophyllum*, were dominated by Asian insects that had low risk ratings despite having phylogenetically related Asian hosts. Comparatively, moderate and high risk ratings were clustered primarily within Salicaceae, Betulaceae, and selected genera within Pinaceae (Figure 4, Figure 5). Pacific Northwest angiosperm hosts contained substantially more Asian insects with moderate and high risk ratings relative to gymnosperm hosts, whereas gymnosperm hosts were dominated by Asian insects with low risk ratings (Figure 4, Figure 5).

Discussion

The observed invasion risk patterns demonstrate how the divergence times between Asian and Pacific Northwest host trees can play a role in structuring the invasiveness of Asian forest insects on Pacific Northwestern host trees. Across both angiosperm and gymnosperm host-pair matrices, Asian insects with a moderate or high risk rating were not randomly distributed, but instead clustered within certain host lineages. Previous modeling efforts on which this chapter was based underscored the importance of evolutionary history in affecting the invasiveness of introduced insect herbivores (Mech et al. 2019, Schulz et al. 2021, Uden et al. 2022, Schulz et al. 2025). Specifically, closely related host species are hypothesized to retain conserved morphological, chemical, and phenological defensive traits that are still effective against an introduced insect, while very distantly related host species are not considered as suitable hosts. Under this modeling framework, it is hypothesized that there is a "goldilocks" range of divergence times in which host plants have lost effective defensive responses against an introduced insect, while still being similar enough to the evolutionarily-native host plant to be recognized as a suitable host plant in the introduced range. This study extends previous work that was exclusively focused on

the risk from insects native to Europe (Uden et al. 2022) by considering insects native to Asia and their risk to Pacific Northwestern host trees.

The dominance of Lepidoptera and Coleoptera within the Asian focus assemblage (Figure 1) further supports the importance of host conservatism in determining invasion potential. These orders contain many specialized folivorous and xylophagous taxa whose host use is often strongly constrained by plant defensive chemistry and tissue structure (Ohmart 1989, Forister et al. 2015, Ulyshen 2018). The prevalence of folivores in particular suggests that many of the focal insects rely on conserved leaf traits that may persist across closely related temperate tree species. Consequently, insects associated with Asian hosts that diverged relatively recently from Pacific Northwestern hosts may encounter fewer physiological barriers to successful establishment, and subsequent ecological and economic impacts.

Among angiosperms, the most high risk ratings of Asian insects occurred primarily within *Betula* and *Populus*, while extensive clusters of moderate risk ratings occurred within *Salix* (Figure 3). These genera are broadly distributed across the Northern Hemisphere and are known to support diverse insect herbivore communities in both Asia and North America (Southwood 1961, Stettler et al. 1996, Whitham et al. 2006). The relatively large number of Asian insects that feed in these plant genera that were assigned a moderate or high risk rating could reflect relatively recent divergence times between their respective Asian and North American lineages compared to more distantly related host groups. Because many structural and chemical host traits remain conserved over shorter evolutionary timescales, associated herbivores may require relatively little adaptation to exploit novel host congeners or sister taxa following their successful introduction.

The concentration of Asian insects with moderate risk ratings within *Acer*, *Alnus*, *Malus*, *Prunus*, *Quercus*, and *Fraxinus* (Figure 3) further supports divergence time as an important predictor of

host suitability. These genera frequently showed evidence of partial compatibility, suggesting that intermediate evolutionary distances may permit limited host utilization even when complete compatibility is absent. In this context, these moderate risk ratings may represent cases in which some ancestral host traits remain conserved, but sufficient divergence has occurred to reduce optimal herbivore performance. This intermediate compatibility may be especially important from a biosecurity perspective because they could facilitate future adaptation or host -range expansion following introduction.

Only one species of Oak, Garry oak (*Quercus garryana*), occurs in the Pacific Northwest, while Asia is a biodiversity hotspot for *Quercus* species. Consequently, there are a great number of potential insect threats identified in this literature review. Garry oak (*Quercus garryana*) ecosystems are among the most threatened terrestrial ecosystems in the Pacific Northwest due to extensive habitat loss, fragmentation, and fire suppression (McCune et al. 2013). Historically maintained by Indigenous burning practices and periodic low-intensity fire, many Garry oak woodlands have experienced encroachment by Douglas-fir and other conifers, leading to reduced open-canopy habitat and declines in associated understory biodiversity. Because Garry oak ecosystems support a disproportionately high number of rare and endemic plant and insect species, continued degradation poses significant risks to regional biodiversity and ecosystem function (Fuchs 2001, Pellatt et al. 2007). The insects utilizing *Quercus* identified in this study should be prioritized for surveillance, quarantine, and early detection to protect this tree and its associated ecosystem.

The high numbers of both high and moderate risk interactions in the family Salicaceae, as well as the high number of Asian insects that use them as hosts, indicates the need to also prioritize these species for surveillance, quarantine, and early detection. *Populus* and *Salix* species are

ecologically important in the Pacific Northwest, where they contribute disproportionately to riparian forest structure and function. Species such as black cottonwood (*Populus trichocarpa*) and willows (*Salix* spp.) are foundational in floodplain and riparian systems, stabilizing soils, enhancing nutrient cycling, and providing critical habitat for birds, insects, and aquatic organisms (Hibbs et al., 2003, Naiman et al., 2005). Their ecological importance also extends to trophic networks, as they host diverse herbivorous insects and associated natural enemies, making them disproportionately influential in shaping riparian biodiversity and potential pest–host interactions in the region (Wootton 1992, Naiman et al. 2005).

The relatively small number of Asian insects with a high risk rating likely reflects the narrow divergence threshold used to define this category. High risk ratings corresponded to host pairs with recent and narrowly constrained evolutionary separation, for which there was only a limited number of Asian–Pacific Northwest pairings. However, this finding is not surprising given that only a minority of introduced insect herbivores are associated with ecological or economic impacts. For example, Aukema et al. (2010) estimated that ~20% of introduced forest insects in North America had any documented impacts to host plants, and Mech et al. (2019) estimate that only ~10% of introduced conifer specialists caused high impacts in their host plants. Nevertheless, the repeated appearance of *Betula* and *Populus* within the high risk rating category (Figure 3) suggests particularly strong evolutionary conservatism within these genera. In contrast, *Quercus* exhibited primarily moderate risk ratings despite substantial herbivore diversity. This pattern may indicate greater divergence in defensive chemistry or ecological traits between Asian and North American *Quercus* lineages, reducing full host compatibility despite phylogenetic relatedness.

Gymnosperm hosts exhibited a markedly different pattern from angiosperm hosts. Asian insects with high risk ratings were not detected, and most Asian insects on gymnosperms were rated in the moderate or low risk categories (Figure 4). Moderate risk ratings of Asian insects occurred primarily within *Abies* and *Larix*, while *Pinus* and *Picea* were dominated by low risk ratings. This pattern may reflect stronger host conservatism and specialization among conifer-feeding insects, which are often tightly associated with resin chemistry and lineage-specific defensive compounds (Ohmart 1989). Greater evolutionary divergence among Northern Hemisphere conifer lineages may therefore create stronger host suitability barriers for introduced insects compared with angiosperm hosts. Alternatively, the lower number of Asian insects with high risk ratings on gymnosperms may partly reflect incomplete representation of compatible conifer-associated insects within the available literature.

Overall, these findings showcase how divergence times between Asian and Pacific Northwest host trees provides a useful framework for predicting the potential invasion risk by herbivorous forest insects native to Asia. Host plant genera with relatively recent evolutionary separation from their Asian relatives, particularly within Salicaceae and Betulaceae, appear most vulnerable to impact from introduced herbivores. In contrast, more distantly related or chemically divergent hosts exhibit substantially lower inferred susceptibility of high impacts. The strong phylogenetic structure observed across both angiosperm and gymnosperm hosts provides an important basis for prioritizing surveillance, quarantine, and early detection efforts targeting future forest insect invasions in western North America.

Afterword

Despite the large number of insects within the Asian focus assemblage (n=368), the dataset must be considered as a subset of the total insects in Asia and cannot by any means be considered complete. The shortcomings of the Asian focus assemblage can be looked at through the lens of the former United States Secretary of Defense, Donald Rumsfeld, in his news briefing on February 12, 2002, "because as we know, there are known knowns; there are things we know we know. We also know there are known unknowns; that is to say we know there are some things we do not know. But there are also unknown unknowns—the ones we don't know we don't know." The known knowns are supplied by the many excellent entomological and botanical resources (e.g. Xiao 1992, Ji et al. 2011, Musolin et al. 2022, Choi et al. 2019, Lee et al. 2012, Appendix 2). I also found many known unknowns in the form of insect records with very little information other than occurrence data, or only having been caught in traps with no reference to host plants. Finally, there are surely many unknown unknown insects dwelling in the forests of Asia. They are likely feeding on non-economically important trees or doing little damage to attract the attention of forest managers or entomologists, never making their way into the scientific literature despite their hidden potential to cause high impacts in an introduced area (i.e., the emerald ash borer, *Agrilus planipennis* Fairmaire, which received extremely little attention in its native Asia until it was introduced into North America where it will likely lead to the functional extinction of North American *Fraxinus* spp. (Herms & McCullough 2014)).

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Tables

Table 3-1: List of host tree species of Pacific Northwestern forests.

Class	Family	Species
Angiosperm	Betulaceae	Alnus rubra
Angiosperm	Betulaceae	Alnus viridis ssp. sinuate
Angiosperm	Betulaceae	Alnus incana ssp. tenuifolia
Angiosperm	Betulaceae	Betula papyrifera
Angiosperm	Betulaceae	Quercus garryana
Angiosperm	Salicaceae	Salix hookeriana
Angiosperm	Salicaceae	Salix lucida ssp. lasiandra
Angiosperm	Salicaceae	Salix scouleriana
Angiosperm	Salicaceae	Salix sitchensis
Angiosperm	Salicaceae	Populus balsamifera L. ssp. trichocarpa
Angiosperm	Salicaceae	Populus tremuloides
Angiosperm	Rosaceae	Malus fusca
Angiosperm	Rosaceae	Prunus emarginata
Angiosperm	Rosaceae	Prunus virginiana
Angiosperm	Rosaceae	Crataegus douglasii
Angiosperm	Rosaceae	Crataegus suksdorfii
Angiosperm	Cornaceae	Cornus nuttallii
Angiosperm	Aceraceae	Acer macrophyllum
Angiosperm	Aceraceae	Acer circinatum
Angiosperm	Aceraceae	Acer glabrum var. douglasii
Angiosperm	Oleaceae	Fraxinus latifolia
Gymnosperm	Pinaceae	Pseudotsuga menziesii
Gymnosperm	Pinaceae	Tsuga heterophylla
Gymnosperm	Pinaceae	Tsuga mertensiana
Gymnosperm	Pinaceae	Picea sitchensis
Gymnosperm	Pinaceae	Picea engelmannii
Gymnosperm	Pinaceae	Abies grandis
Gymnosperm	Pinaceae	Abies procera
Gymnosperm	Pinaceae	Abies amabilis
Gymnosperm	Pinaceae	Abies lasiocarpa
Gymnosperm	Pinaceae	Pinus monticola
Gymnosperm	Pinaceae	Pinus contorta
Gymnosperm	Pinaceae	Pinus ponderosa
Gymnosperm	Pinaceae	Larix occidentalis
Gymnosperm	Cupressaceae	Thuja plicata
Gymnosperm	Cupressaceae	Juniperus scopulorum
Gymnosperm	Cupressaceae	Juniperus communis
Gymnosperm	Cupressaceae	Chamaecyparis lawsoniana

Table 3-2: List of host tree species of Asian temperate forests.

Division	Family	Species
Angiosperm	Aceraceae	Acer barbinerve
Angiosperm	Aceraceae	Acer buergerianum
Angiosperm	Aceraceae	Acer carpinifolium
Angiosperm	Aceraceae	Acer crataegifolium
Angiosperm	Aceraceae	Acer distylum
Angiosperm	Aceraceae	Acer japonicum
Angiosperm	Aceraceae	Acer miyabei
Angiosperm	Aceraceae	Acer mono
Angiosperm	Aceraceae	Acer oblongum
Angiosperm	Aceraceae	Acer palmatum
Angiosperm	Aceraceae	Acer pictum
Angiosperm	Aceraceae	Acer pseudosieboldianum
Angiosperm	Aceraceae	Acer rufinerve
Angiosperm	Aceraceae	Acer shirasawanum
Angiosperm	Aceraceae	Acer sieboldianum
Angiosperm	Aceraceae	Acer tataricum
Angiosperm	Aceraceae	Acer truncatum
Angiosperm	Aceraceae	Acer tschonoskii
Angiosperm	Betulaceae	Alnus firma
Angiosperm	Betulaceae	Alnus hirsuta
Angiosperm	Betulaceae	Alnus inokumae
Angiosperm	Betulaceae	Alnus japonica
Angiosperm	Betulaceae	Alnus matsumurae
Angiosperm	Betulaceae	Alnus maximowiczii
Angiosperm	Betulaceae	Alnus pendula
Angiosperm	Betulaceae	Alnus sieboldiana
Angiosperm	Betulaceae	Betula albosinensis
Angiosperm	Betulaceae	Betula ermanii
Angiosperm	Betulaceae	Betula grossa
Angiosperm	Betulaceae	Betula mandshurica
Angiosperm	Betulaceae	Betula maximowicziana
Angiosperm	Betulaceae	Betula platyphylla
Angiosperm	Betulaceae	Betula utilis
Angiosperm	Cornaceae	Cornus alba
Angiosperm	Cornaceae	Cornus controversa
Angiosperm	Cornaceae	Cornus kousa
Angiosperm	Cornaceae	Cornus macrophylla
Angiosperm	Fagaceae	Quercus acutissima
Angiosperm	Fagaceae	Quercus aliena
Angiosperm	Fagaceae	Quercus cerris
Angiosperm	Fagaceae	Quercus chenii
Angiosperm	Fagaceae	Quercus crenata

Table 3-2: (continued)

Division	Family	Species
Angiosperm	Fagaceae	Quercus crispula
Angiosperm	Fagaceae	Quercus dentata
Angiosperm	Fagaceae	Quercus fabrei
Angiosperm	Fagaceae	Quercus gilva
Angiosperm	Fagaceae	Quercus glauca
Angiosperm	Fagaceae	Quercus mongolica
Angiosperm	Fagaceae	Quercus phillyreoides
Angiosperm	Fagaceae	Quercus salicina
Angiosperm	Fagaceae	Quercus serrata
Angiosperm	Fagaceae	Quercus sessilifolia
Angiosperm	Fagaceae	Quercus variabilis
Angiosperm	Fagaceae	Quercus wutaishanica
Angiosperm	Oleaceae	Fraxinus bungeana
Angiosperm	Oleaceae	Fraxinus chinensis
Angiosperm	Oleaceae	Fraxinus lanuginosa
Angiosperm	Oleaceae	Fraxinus longicuspis
Angiosperm	Oleaceae	Fraxinus mandshurica
Angiosperm	Oleaceae	Fraxinus platypoda
Angiosperm	Oleaceae	Fraxinus sieboldiana
Angiosperm	Rosaceae	Crataegus chlorosarca
Angiosperm	Rosaceae	Malus baccata
Angiosperm	Rosaceae	Malus prunifolia
Angiosperm	Rosaceae	Malus pumila
Angiosperm	Rosaceae	Malus sieboldii
Angiosperm	Rosaceae	Malus toringo
Angiosperm	Rosaceae	Malus tschonoskii
Angiosperm	Rosaceae	Prunus armeniaca
Angiosperm	Rosaceae	Prunus avium
Angiosperm	Rosaceae	Prunus buergeriana
Angiosperm	Rosaceae	Prunus grayana
Angiosperm	Rosaceae	Prunus jamasakura
Angiosperm	Rosaceae	Prunus japonica
Angiosperm	Rosaceae	Prunus maximowiczii
Angiosperm	Rosaceae	Prunus mume
Angiosperm	Rosaceae	Prunus persica
Angiosperm	Rosaceae	Prunus salicina
Angiosperm	Rosaceae	Prunus sargentii
Angiosperm	Rosaceae	Prunus serrulata
Angiosperm	Rosaceae	Prunus spinulosa
Angiosperm	Rosaceae	Prunus ssiori
Angiosperm	Rosaceae	Prunus yedoensis
Angiosperm	Rosaceae	Prunus zippeliana

Table 3-2: (continued)

Division	Family	Species
Angiosperm	Salicaceae	Populus alba
Angiosperm	Salicaceae	Populus cathayana
Angiosperm	Salicaceae	Populus euphratica
Angiosperm	Salicaceae	Populus laurifolia
Angiosperm	Salicaceae	Populus maximowiczii
Angiosperm	Salicaceae	Populus pseudoglauca
Angiosperm	Salicaceae	Populus pseudosimonii
Angiosperm	Salicaceae	Populus sieboldii
Angiosperm	Salicaceae	Populus simonii
Angiosperm	Salicaceae	Populus suaveolens
Angiosperm	Salicaceae	Populus tomentosa
Angiosperm	Salicaceae	Populus tomentosa
Angiosperm	Salicaceae	Populus tremula
Angiosperm	Salicaceae	Populus yunnanensis
Angiosperm	Salicaceae	Salix babylonica
Angiosperm	Salicaceae	Salix chaenomeloides
Angiosperm	Salicaceae	Salix dolichostyla
Angiosperm	Salicaceae	Salix gilgiana
Angiosperm	Salicaceae	Salix gordejevii
Angiosperm	Salicaceae	Salix gracilistyla
Angiosperm	Salicaceae	Salix integra
Angiosperm	Salicaceae	Salix japonica
Angiosperm	Salicaceae	Salix matsudana
Angiosperm	Salicaceae	Salix pierotii
Angiosperm	Salicaceae	Salix reinii
Angiosperm	Salicaceae	Salix rorida
Angiosperm	Salicaceae	Salix serissaefolia
Angiosperm	Salicaceae	Salix sieboldiana
Gymnosperm	Cupressaceae	Chamaecyparis formosensis
Gymnosperm	Cupressaceae	Chamaecyparis obtusa
Gymnosperm	Cupressaceae	Chamaecyparis pisifera
Gymnosperm	Cupressaceae	Juniperus chinensis
Gymnosperm	Cupressaceae	Juniperus rigida
Gymnosperm	Cupressaceae	Juniperus squamata
Gymnosperm	Pinaceae	Abies fabri
Gymnosperm	Pinaceae	Abies firma
Gymnosperm	Pinaceae	Abies holophylla
Gymnosperm	Pinaceae	Abies homolepis
Gymnosperm	Pinaceae	Abies mariesii
Gymnosperm	Pinaceae	Abies nephrolepis
Gymnosperm	Pinaceae	Abies sachalinensis
Gymnosperm	Pinaceae	Abies veitchii

Table 3-2: (continued)

Division	Family	Species
Gymnosperm	Pinaceae	Larix gmelinii
Gymnosperm	Pinaceae	Larix kaempferi
Gymnosperm	Pinaceae	Larix leptolepis
Gymnosperm	Pinaceae	Larix olgensis
Gymnosperm	Pinaceae	Larix sibirica
Gymnosperm	Pinaceae	Picea alcoquiana
Gymnosperm	Pinaceae	Picea brachytyla
Gymnosperm	Pinaceae	Picea crassifolia
Gymnosperm	Pinaceae	Picea glehnii
Gymnosperm	Pinaceae	Picea jezoensis
Gymnosperm	Pinaceae	Picea koraiensis
Gymnosperm	Pinaceae	Picea koyamae
Gymnosperm	Pinaceae	Picea likiangensis
Gymnosperm	Pinaceae	Picea maximowiczii
Gymnosperm	Pinaceae	Picea meyeri
Gymnosperm	Pinaceae	Picea polita
Gymnosperm	Pinaceae	Picea purpurea
Gymnosperm	Pinaceae	Picea schrenkiana
Gymnosperm	Pinaceae	Picea shirasawae
Gymnosperm	Pinaceae	Pinus armandii
Gymnosperm	Pinaceae	Pinus densata
Gymnosperm	Pinaceae	Pinus densiflora
Gymnosperm	Pinaceae	Pinus hwangshanensis
Gymnosperm	Pinaceae	Pinus kesiya
Gymnosperm	Pinaceae	Pinus koraiensis
Gymnosperm	Pinaceae	Pinus latteri
Gymnosperm	Pinaceae	Pinus luchuensis
Gymnosperm	Pinaceae	Pinus massoniana
Gymnosperm	Pinaceae	Pinus merkusii
Gymnosperm	Pinaceae	Pinus morrisonicola
Gymnosperm	Pinaceae	Pinus parviflora
Gymnosperm	Pinaceae	Pinus pumila
Gymnosperm	Pinaceae	Pinus sylvestris
Gymnosperm	Pinaceae	Pinus tabuliformis
Gymnosperm	Pinaceae	Pinus taiwanensis
Gymnosperm	Pinaceae	Pinus thunbergii
Gymnosperm	Pinaceae	Pinus wallichiana
Gymnosperm	Pinaceae	Pinus yunnanensis
Gymnosperm	Pinaceae	Pseudotsuga brevifolia
Gymnosperm	Pinaceae	Pseudotsuga forestii
Gymnosperm	Pinaceae	Pseudotsuga japonica
Gymnosperm	Pinaceae	Pseudotsuga sinensis

Table 3-2: (continued)

Division	Family	Species
Gymnosperm	Pinaceae	Thuja koraiensis
Gymnosperm	Pinaceae	Thuja sutchuenensis
Gymnosperm	Pinaceae	Tsuga diversifolia
Gymnosperm	Pinaceae	Tsuga sieboldii

Table 3-3: North American insect genera associated with each Pacific Northwest American tree species (Table 3-1).

Insect Genera (Species)	North American Host Plant Species	Host Tree Family	Insect Order	Insect Family
Agrilus burkei	Alnus rubra	Betulaceae	Coleoptera	Buprestidae
Buprestis adjecta	Pinus contorta	Pinaceae	Coleoptera	Buprestidae
Buprestis adjecta	Pinus ponderosa	Pinaceae	Coleoptera	Buprestidae
Buprestis aurulenta	Pinus ponderosa	Pinaceae	Coleoptera	Buprestidae
Buprestis intricata	Pinus contorta	Pinaceae	Coleoptera	Buprestidae
Buprestis laevirentris	Pinus ponderosa	Pinaceae	Coleoptera	Buprestidae
Buprestis laeviventris	Pinus contorta	Pinaceae	Coleoptera	Buprestidae
Buprestis subornata	Pinus ponderosa	Pinaceae	Coleoptera	Buprestidae
Buprestis subronata	Pinus contorta	Pinaceae	Coleoptera	Buprestidae
Chryosobothris eaurina	Pinus ponderosa	Pinaceae	Coleoptera	Buprestidae
Dendroctonus brevicomis	Pinus ponderosa	Pinaceae	Coleoptera	Scolytinae
Dendroctonus jeffreyi	Pinus ponderosa	Pinaceae	Coleoptera	Scolytinae
Dendroctonus murrayanae	Pinus contorta	Pinaceae	Coleoptera	Curculionidae
Dendroctonus ponderosae	Pinus contorta	Pinaceae	Coleoptera	Curculionidae
Dendroctonus ponderosae	Pinus monticola	Pinaceae	Coleoptera	Curculionidae
Dendroctonus ponderosae	Pinus ponderosa	Pinaceae	Coleoptera	Scolytinae
Dendroctonus pseudotsugae	Pseudotsuga menziesii	Pinaceae	Coleoptera	Curculionidae
Dendroctonus valens	Pinus contorta	Pinaceae	Coleoptera	Curculionidae
Dendroctonus valens	Pinus monticola	Pinaceae	Coleoptera	Curculionidae
Dendroctonus valens	Pinus ponderosa	Pinaceae	Coleoptera	Scolytinae
Ips concinnus	Picea sitchensis	Pinaceae	Coleoptera	Curculionidae
Ips cribrieollis	Pinus ponderosa	Pinaceae	Coleoptera	Curculionidae
Ips emarginatus	Pinus contorta	Pinaceae	Coleoptera	Curculionidae
Ips emarginatus	Pinus monticola	Pinaceae	Coleoptera	Curculionidae
Ips emarginatus	Pinus ponderosa	Pinaceae	Coleoptera	Curculionidae
Ips integer	Pinus contorta	Pinaceae	Coleoptera	Curculionidae
Ips interstitialis	Pinus ponderosa	Pinaceae	Coleoptera	Curculionidae
Ips latidens	Pinus contorta	Pinaceae	Coleoptera	Curculionidae
Ips latidens	Pinus contorta	Pinaceae	Coleoptera	Curculionidae
Ips latidens	Pinus monticola	Pinaceae	Coleoptera	Curculionidae
Ips latidens	Pinus ponderosa	Pinaceae	Coleoptera	Curculionidae
Ips montanus	Pinus contorta	Pinaceae	Coleoptera	Curculionidae
Ips montanus	Pinus monticola	Pinaceae	Coleoptera	Curculionidae
Ips paraconfusus	Pinus contorta	Pinaceae	Coleoptera	Curculionidae

Table 3-1: (continued)

Insect Genera (Species)	North American Host Plant Species	Host Tree Family	Insect Order	Insect Family
Ips paraconfusus	Pinus monticola	Pinaceae	Coleoptera	Curculionidae
Ips paraconfusus	Pinus ponderosa	Pinaceae	Coleoptera	Curculionidae
Ips perroli	Pinus contorta	Pinaceae	Coleoptera	Curculionidae
Ips pilifrons thatcheri	Pinus ponderosa	Pinaceae	Coleoptera	Curculionidae
Ips pini	Pinus contorta	Pinaceae	Coleoptera	Curculionidae
Ips pini	Pinus ponderosa	Pinaceae	Coleoptera	Curculionidae
Ips plastographus	Larix occidentalis	Pinaceae	Coleoptera	Curculionidae
Ips plastographus	Picea sitchensis	Pinaceae	Coleoptera	Curculionidae
Ips tridens	Picea sitchensis	Pinaceae	Coleoptera	Curculionidae
Melanophila acuminata	Pinus contorta	Pinaceae	Coleoptera	Buprestidae
Melanophila acuminata	Pinus ponderosa	Pinaceae	Coleoptera	Buprestidae
Melanophila californica	Pinus ponderosa	Pinaceae	Coleoptera	Buprestidae
Melanophila consputa	Pinus contorta	Pinaceae	Coleoptera	Buprestidae
Melanophila consputa	Pinus ponderosa	Pinaceae	Coleoptera	Buprestidae
Melanophila drummondi	Larix occidentalis	Pinaceae	Coleoptera	Buprestidae
Melanophila gentilis	Pinus ponderosa	Pinaceae	Coleoptera	Buprestidae
Semanotus amethystinus	Thuja plicata	Cupressaceae	Coleoptera	Cerambycidae
Adelges cooleyi	Picea sitchensis	Pinaceae	Hemiptera	Adelgidae
Adelges ishiharai	Picea sitchensis	Pinaceae	Hemiptera	Adelgidae
Adelges oregonensis	Larix occidentalis	Pinaceae	Hemiptera	Adelgidae
Cinara azteca	Pinus ponderosa	Pinaceae	Hemiptera	Aphididae
Cinara brevispinosa	Pinus contorta	Pinaceae	Hemiptera	Aphididae
Cinara canatra	Pinus contorta	Pinaceae	Hemiptera	Aphididae
Cinara contortae	Pinus contorta	Pinaceae	Hemiptera	Aphididae
Cinara costata	Picea sitchensis	Pinaceae	Hemiptera	Aphididae
Cinara curvipes	Pinus contorta	Pinaceae	Hemiptera	Aphididae
Cinara ferrisi	Pinus monticola	Pinaceae	Hemiptera	Aphididae
Cinara glabra	Pinus ponderosa	Pinaceae	Hemiptera	Aphididae
Cinara hirsuta	Pinus monticola	Pinaceae	Hemiptera	Aphididae
Cinara kuchea	Pinus monticola	Pinaceae	Hemiptera	Aphididae
Cinara medispinosa	Pinus contorta	Pinaceae	Hemiptera	Aphididae
Cinara murrayanae	Pinus contorta	Pinaceae	Hemiptera	Aphididae
Cinara nigra	Pinus contorta	Pinaceae	Hemiptera	Aphididae
Cinara oregonensis	Pinus contorta	Pinaceae	Hemiptera	Aphididae
Cinara oregonensis	Pinus ponderosa	Pinaceae	Hemiptera	Aphididae
Cinara parvicornis	Pinus contorta	Pinaceae	Hemiptera	Aphididae
Cinara pergandei	Pinus contorta	Pinaceae	Hemiptera	Aphididae

Table 3-1: (continued)

Insect Genera (Species)	North American Host Plant Species	Host Tree Family	Insect Order	Insect Family
Cinara pini	Pinus ponderosa	Pinaceae	Hemiptera	Aphididae
Cinara piniradiatae	Pinus contorta	Pinaceae	Hemiptera	Aphididae
Cinara ponderosae	Pinus ponderosa	Pinaceae	Hemiptera	Aphididae
Cinara schwarzii	Pinus ponderosa	Pinaceae	Hemiptera	Aphididae
Cinara solitaria	Pinus ponderosa	Pinaceae	Hemiptera	Aphididae
Cinara thatcheri	Pinus ponderosa	Pinaceae	Hemiptera	Aphididae
Kermes cockerelli	Quercus garryana	Betulaceae	Hemiptera	Kermesidae
Kermes rimarum	Quercus garryana	Betulaceae	Hemiptera	Kermesidae
Matsucoccus bisetosus	Pinus contorta	Pinaceae	Hemiptera	Matsucoccidae
Matsucoccus fasciculensis	Pinus contorta	Pinaceae	Hemiptera	Matsucoccidae
Matsucoccus paucicicatrices	Pinus monticola	Pinaceae	Hemiptera	Matsucoccidae
Pineus coloradensis	Pinus contorta	Pinaceae	Hemiptera	Adelgidae
Pineus coloradensis	Pinus monticola	Pinaceae	Hemiptera	Adelgidae
Pineus coloradensis	Pinus ponderosa	Pinaceae	Hemiptera	Adelgidae
Pineus harvrylenkoi	Pinus contorta	Pinaceae	Hemiptera	Adelgidae
Pineus pinifoliae	Picea sitchensis	Pinaceae	Hemiptera	Adelgidae
Pineus similis	Picea sitchensis	Pinaceae	Hemiptera	Adelgidae
Prociphilus americanus	Fraxinus latifolia	Oleaceae	Hemiptera	Aphididae
Acantholyda albomarginara	Pinus ponderosa	Pinaceae	Hymenoptera	Pamphiliidae
Acantholyda brunnicans	Pinus contorta	Pinaceae	Hymenoptera	Pamphiliidae
Acantholyda verticalis	Pinus contorta	Pinaceae	Hymenoptera	Pamphiliidae
Acantholyda verticalis	Pinus monticola	Pinaceae	Hymenoptera	Pamphiliidae
Acantholyda verticalis	Pinus ponderosa	Pinaceae	Hymenoptera	Pamphiliidae
Anoplonyx laricivorous	Larix occidentalis	Pinaceae	Hymenoptera	Tenthredinidae
Anoplonyx occidens	Larix occidentalis	Pinaceae	Hymenoptera	Tenthredinidae
Cephalcia californica	Pinus ponderosa	Pinaceae	Hymenoptera	Pamphiliidae
Neodiprion fulviceps	Pinus monticola	Pinaceae	Hymenoptera	Diprionidae
Neodiprion fulviceps	Pinus ponderosa	Pinaceae	Hymenoptera	Diprionidae
Neodiprion mundus	Pinus ponderosa	Pinaceae	Hymenoptera	Diprionidae
Neodiprion nanulus contortae	Pinus contorta	Pinaceae	Hymenoptera	Diprionidae
Argyresthia columbia	Larix occidentalis	Pinaceae	Lepidoptera	Argyresthiidae
Bucculatrix zophopasta	Quercus garryana	Betulaceae	Lepidoptera	Bucculatricidae
Rhyacionia multilineata	Pinus ponderosa	Pinaceae	Lepidoptera	Tortricidae
Rhyacionia subcervinana	Pinus ponderosa	Pinaceae	Lepidoptera	Tortricidae
Rhyacionia zozana	Pinus contorta	Pinaceae	Lepidoptera	Tortricidae
Rhyacionia zozana	Pinus ponderosa	Pinaceae	Lepidoptera	Tortricidae
Ypsolopha cervella	Quercus garryana	Betulaceae	Lepidoptera	Ypsolophidae

Table 3-4: List of Pacific Northwest native trees and the number of risk associations.

Species	Highest risk: North American congener present	High risk: North American congener present	Moderate risk: no North American congener present	Moderate risk: North American congener present	Low risk: no North American congener present	Lowest risk: North American congener present
Abies amabilis					1	
Abies grandis					1	
Abies lasiocarpa			21			
Abies procera					1	
Acer circinatum			19		42	
Acer glabrum var. douglasii					41	
Acer macrophyllum					41	
Alnus rubra			47	2		
Alnus incana ssp. tenuifolia			44	1	27	1
Alnus sinuata	3		50	1	20	1
Betula papyrifera	5		26			
Chamaecyparis lawsoniana					3	
Cornus nuttallii			1		3	
Crataegus douglasii			1			
Crataegus suksdorfii			1			
Fraxinus latifolia			18	5		
Juniperus communis			3			
Juniperus scopulorum			3			
Larix occidentalis			17	9		
Malus fusca			20			
Picea engelmannii				1	13	9
Picea sitchensis					18	5
Pinus contorta					83	40
Pinus monticola					83	40
Pinus ponderosa					83	40
Populus balsamifera L. ssp. trichocarpa	8		23			
Populus tremuloides			21			
Prunus emarginata			2		44	
Prunus virginiana			6		44	
Pseudotsuga menziesii				1		
Quercus garryana			204	10	58	4
Salix hookeriana			13			
Salix lucida ssp. lasiandra			20			
Salix scouleriana			10			
Salix sitchensis			12			
Thuja plicata			1	1		
Tsuga heterophylla					4	
Tsuga mertensiana					4	

Figures

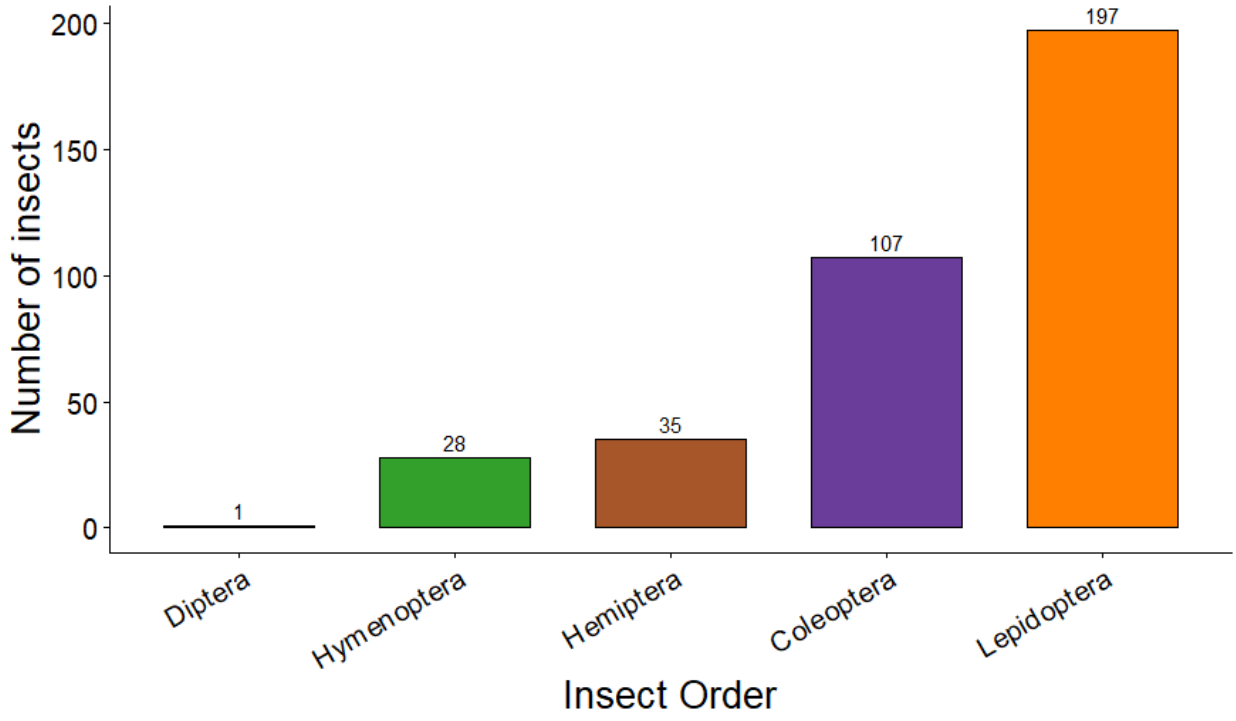

Figure 3-1: Number of insects belonging to each Order in the Asian focus assemblage.

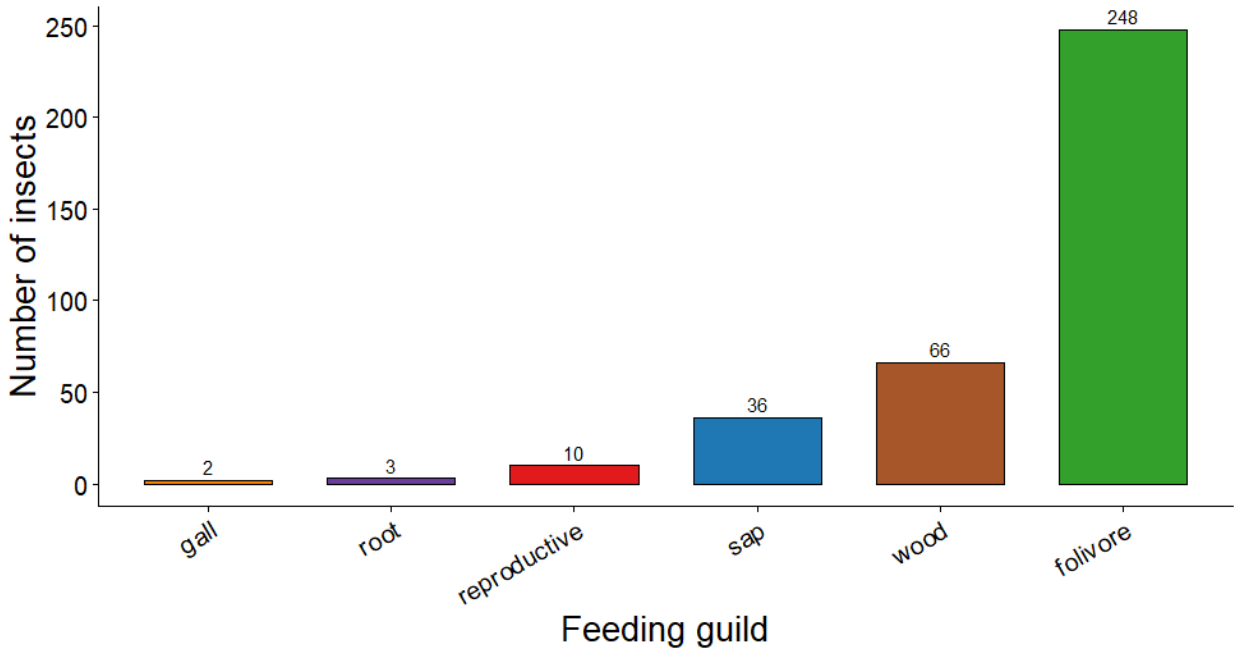

Figure 3-2: Number of insects in each feeding guild within the Asian focus assemblage.

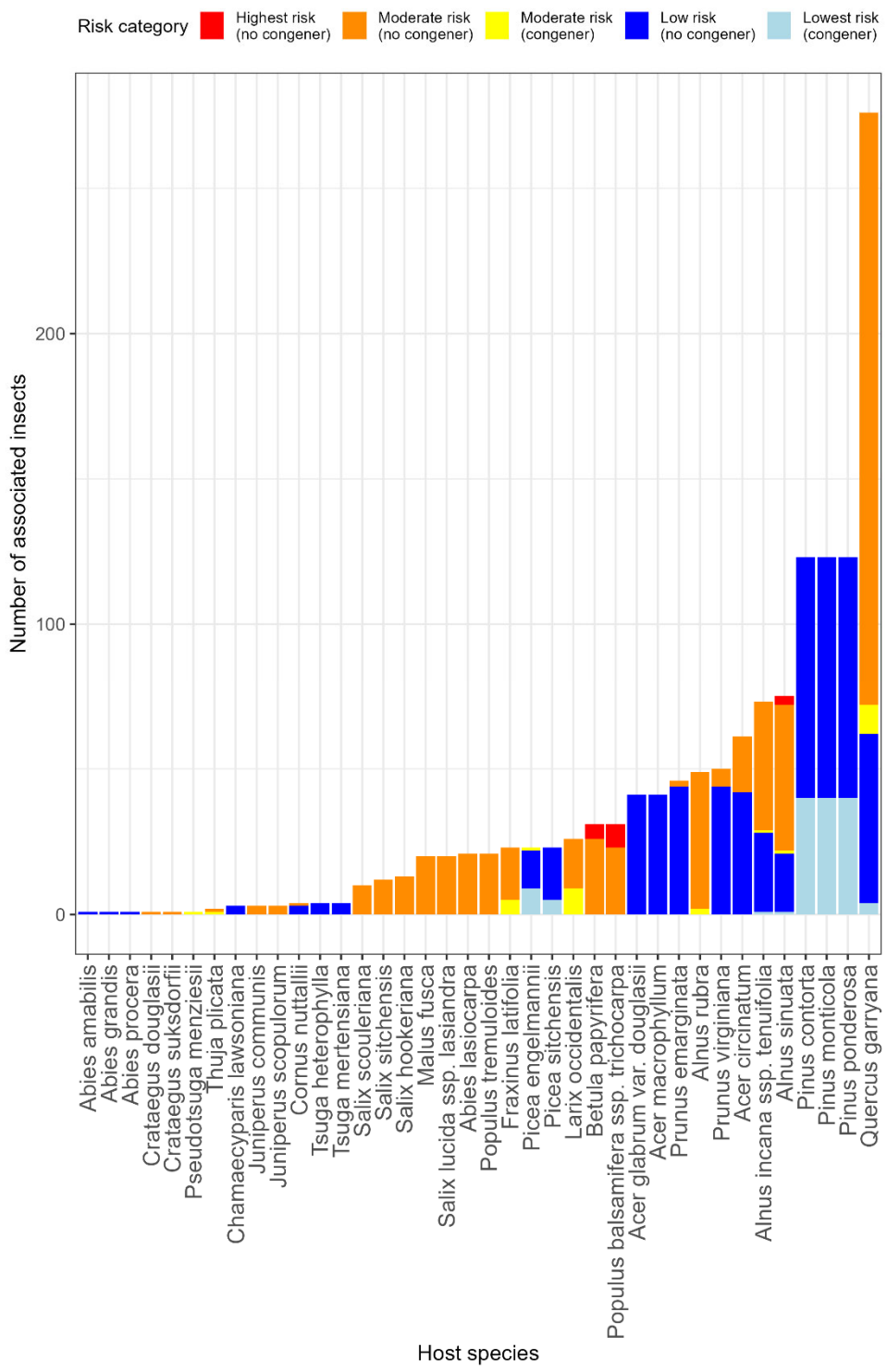

Figure 3-3: Stacked bar chart of Pacific Northwest native trees and the number of Asian insects and their associated risk associations.

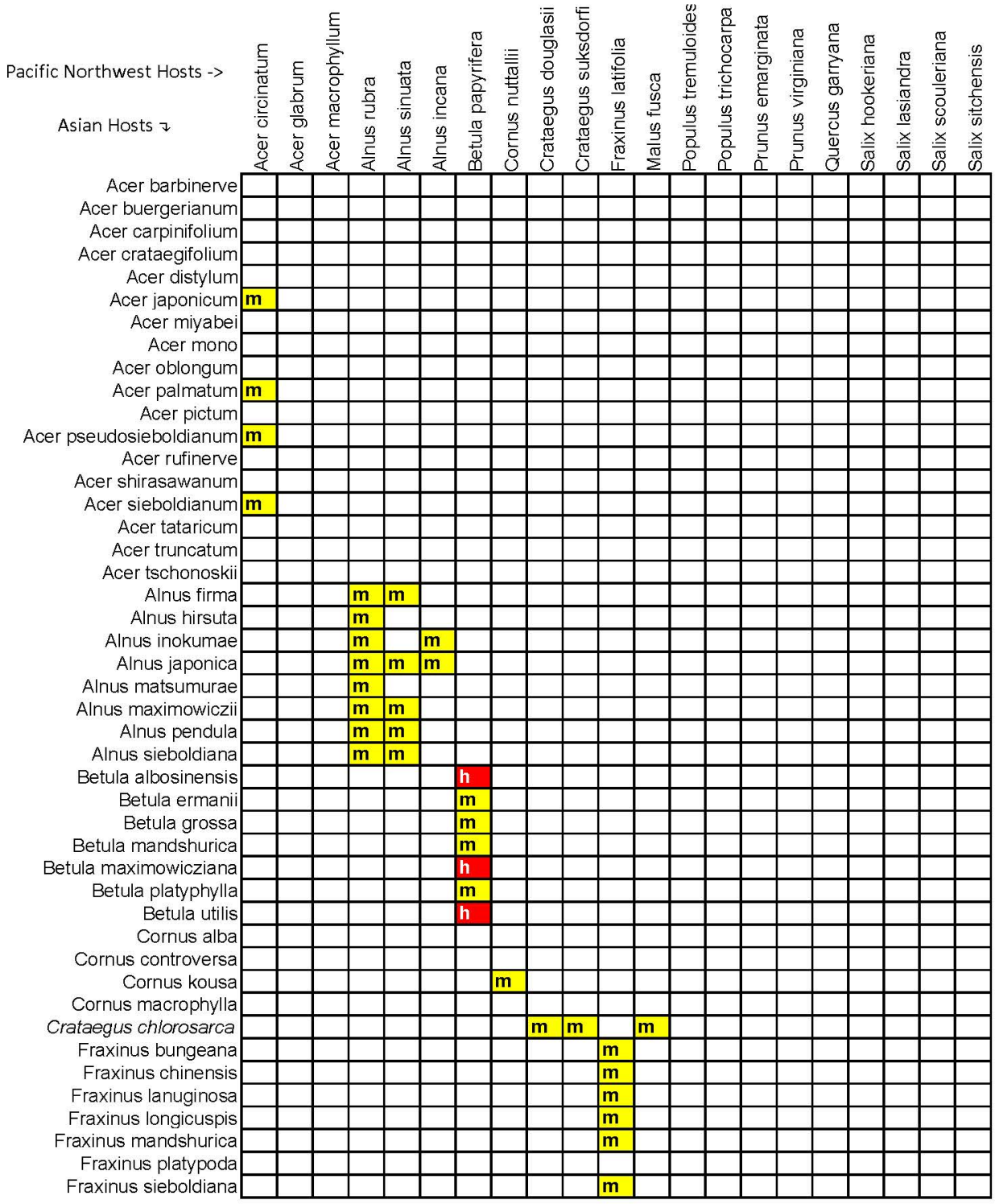

Figure 3-4: Matrix of Pacific Northwest and Asian angiosperms with their pairwise potential impact rating. Blank cells are low impact risk ratings, yellow highlighted cells are moderate impact risk ratings, and red are high risk ratings.

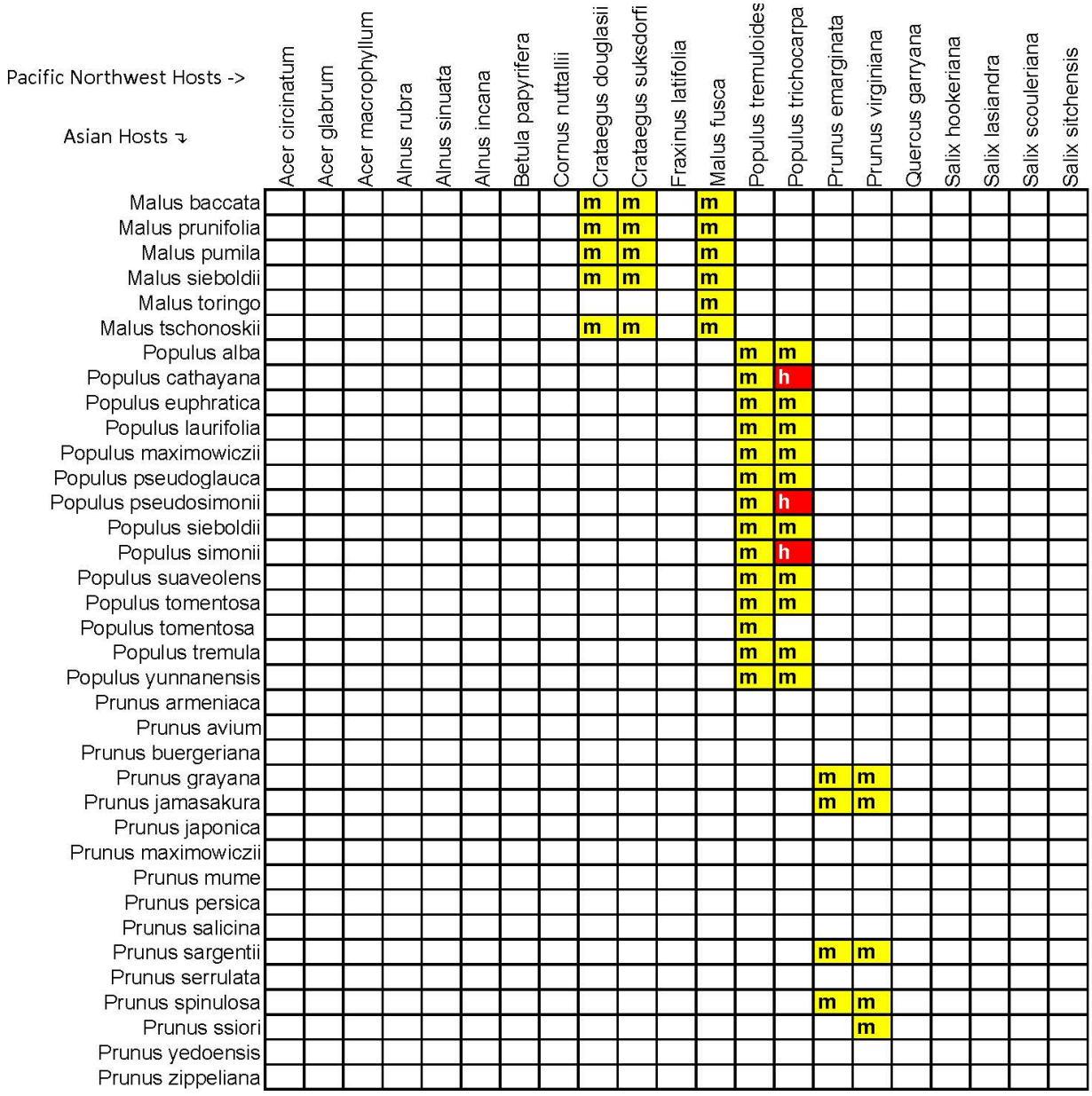

Figure 3-4: (continued)

Pacific Northwest Hosts -> / Asian Hosts ↴	Acer circinatum	Acer glabrum	Acer macrophyllum	Alnus rubra	Alnus sinuata	Alnus incana	Betula papyrifera	Cornus nuttallii	Crataegus douglasii	Crataegus suksdorfi	Fraxinus latifolia	Malus fusca	Populus tremuloides	Populus trichocarpa	Prunus emarginata	Prunus virginiana	Quercus garryana	Salix hookeriana	Salix lasiandra	Salix scouleriana	Salix sitchensis
Quercus acutissima																	m				
Quercus aliena																	m				
Quercus cerris																	m				
Quercus chenii																	m				
Quercus crenata																	m				
Quercus crispula																	m				
Quercus dentata																	m				
Quercus fabrei																	m				
Quercus gilva																	m				
Quercus glauca																	m				
Quercus mongolica																	m				
Quercus phillyreoides																	m				
Quercus salicina																	m				
Quercus serrata																					
Quercus sessilifolia																	m				
Quercus variabilis																	m				
Quercus wutaishanica																	m				
Salix babylonica																			m		
Salix chaenomeloides																			m		
Salix dolichostyla																		m	m		m
Salix gilgiana																		m	m		m
Salix gordejevii																			m		
Salix gracilistyla																		m		m	m
Salix integra																			m	m	
Salix japonica																		m	m		m
Salix matsudana																			m		
Salix pierotii																		m	m	m	m
Salix reinii																			m	m	
Salix rorida																		m		m	m
Salix serissaefolia																			m		
Salix sieboldiana																		m		m	m

Figure 3-4: (continued)

Pacific Northwest Hosts -> / Asian Hosts ↴	Abies amabilis	Abies grandis	Abies lasiocarpa	Abies procera	Chamaecyparis lawsoniana	Juniperus communis	Juniperus scopulorum	Larix occidentalis	Picea engelmannii	Picea sitchensis	Pinus contorta	Pinus monticola	Pinus ponderosa	Pseudotsuga menziesii	Tsuga heterophylla	Tsuga mertensiana	Thuja plicata
Abies fabri			m														
Abies firma			m														
Abies holophylla			m														
Abies homolepis			m														
Abies mariesii																	
Abies nephrolepis			m														
Abies sachalinensis			m														
Abies veitchii			m														
Chamaecyparis formosensis																	
Chamaecyparis obtusa																	
Chamaecyparis pisifera																	
Juniperus chinensis																	
Juniperus rigida							m										
Juniperus squamata																	
Larix gmelinii								m									
Larix kaempferi								m									
Larix leptolepis								m									
Larix olgensis								m									
Larix sibirica								m									
Picea alcoquiana																	
Picea brachytyla									m								
Picea crassifolia																	
Picea glehnii																	
Picea jezoensis																	
Picea koraiensis																	
Picea koyamae																	
Picea likiangensis									m								
Picea maximowiczii									m								
Picea meyeri																	
Picea polita									m								
Picea purpurea									m								
Picea schrenkiana									m								
Picea shirasawae																	

Figure 3-5: Matrix of Pacific Northwest and Asian gymnosperms with their pairwise potential impact rating. Blank cells are low impact risk ratings, yellow are moderate impact risk ratings, and red are high impact ratings.

Pacific Northwest Hosts -> / Asian Hosts ↴	Abies amabilis	Abies grandis	Abies lasiocarpa	Abies procera	Chamaecyparis lawsoniana	Juniperus communis	Juniperus scopulorum	Larix occidentalis	Picea engelmannii	Picea sitchensis	Pinus contorta	Pinus monticola	Pinus ponderosa	Pseudotsuga menziesii	Tsuga heterophylla	Tsuga mertensiana	Thuja plicata
Pinus armandii																	
Pinus densata																	
Pinus densiflora																	
Pinus hwangshanensis																	
Pinus kesiya																	
Pinus koraiensis																	
Pinus latteri																	
Pinus luchuensis																	
Pinus massoniana																	
Pinus merkusii																	
Pinus morrisonicola																	
Pinus parviflora																	
Pinus pumila																	
Pinus sylvestris																	
Pinus tabuliformis																	
Pinus taiwanensis																	
Pinus thunbergii																	
Pinus wallichiana																	
Pinus yunnanensis																	
Pseudotsuga brevifolia														m			
Pseudotsuga forestii														m			
Pseudotsuga japonica														m			
Pseudotsuga sinensis														m			
Thuja koraiensis																	m
Thuja sutchuenensis																	m
Tsuga diversifolia																	
Tsuga sieboldii																	

Figure 3-5: (continued)

Appendix 1: Asian insect species

List of Asian insect species (with Order and Family), their tree hosts, feeding guild, presence of a North American congener, and risk rating. Risks are rated low (l), moderate (m), and high (h).

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Coleoptera	Buprestidae	Agrilus asiaticus	*Quercus variabilis, Quercus acutissima*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Agrilus cyaneoniger	*Quercus crispula, Quercus acutissima, Quercus serrata, Quercus variabilis*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Agrilus fleischeri	*Populus tremula, Populus laurifolia*	*wood*	*n*	*l*
Coleoptera	Buprestidae	Agrilus friebi	*Quercus acutissima, Quercus crispula, Quercus serrata*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Agrilus hattorii	*Quercus acutissima, Quercus crispula, Quercus serrata, Quercus dentata*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Agrilus japanocarinatus	*Fraxinus mandshurica*	*wood*	*y*	*l*
Coleoptera	Buprestidae	Agrilus mali	*Malus spp.*	*wood*	*n*	*l*
Coleoptera	Buprestidae	Agrilus moerens	*Quercus serrata, Quercus crispula, Quercus dentata, Quercus acutissima*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Agrilus motobuanus	*Acer itoanum*	*wood*	*n*	*l*
Coleoptera	Buprestidae	Agrilus nicolanus	*Quercus acutissima*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Agrilus ogatai	Acer spp.	*wood*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Coleoptera	Buprestidae	Agrilus sachalinicola	*Alnus hirsuta*	*wood*	*y*	*l*
Coleoptera	Buprestidae	Agrilus sibiricus subsp. fukushimensis	Acer spp.	*wood*	*n*	*m*
Coleoptera	Buprestidae	Agrilus sospes	*Quercus dentata*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Agrilus sudai	*Alnus hirsuta*	*wood*	*y*	*l*
Coleoptera	Buprestidae	Agrilus tokyoensis	*Quercus acutissima*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Agrilus viridiobscurus	*Alnus pendula*	*wood*	*y*	*l*
Coleoptera	Buprestidae	Anthaxia arakii	*Pinus luchuensis*	*wood*	*n*	*l*
Coleoptera	Buprestidae	Anthaxia ihanatsumi	*Pinus luchuensis*	*wood*	*n*	*l*
Coleoptera	Buprestidae	Anthaxia moya	*Pinus luchuensis*	*wood*	*n*	*l*
Coleoptera	Buprestidae	Anthaxia proteus	*Pinus densiflora*	*wood*	*n*	*l*
Coleoptera	Buprestidae	Anthaxia reticulata	*Abies sachalinensis*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Anthaxia rubromarginata	*Quercus serrata, Quercus acutissima, Quercus variabilis*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Buprestis esakii	*Pinus luchuensis*	*wood*	*y*	*l*
Coleoptera	Buprestidae	Chalcophora japonica	*Pinus densiflora, Pinus thunbergii, Pinus luchuensis*	*wood*	*n*	*l*
Coleoptera	Buprestidae	Chalcophora yunnana	*Pinus latteri, Pinus densiflora, Pinus thunbergii, Pinus luchuensis*	*wood*	*n*	*l*
Coleoptera	Buprestidae	Chrysobothris amurensis	*Acer sieboldianum, Betula ermanii*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Chrysobothris igai	*Pinus densiflora, Abies firma*	*wood*	*y*	*m*
Coleoptera	Buprestidae	Chrysobothris ohbayashii	*Quercus acutissima, Quercus acuta*	*wood*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Coleoptera	Buprestidae	Chrysobothris samurai	*Quercus variabilis*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Chrysobothris succedanea	*Abies firma, Prunus mume, Prunus × yedoensis*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Chrysodema lewisii	*Quercus phillyraeoides*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Coraebus nigromaculatus	*Quercus crispula*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Coraebus rusticanus	*Alnus hirsuta, Alnus firma, Alnus sieboldiana, Betula maximowicziana*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Dicerca tibialis	*Abies firma, Tsuga sieboldii*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Eurythyrea tenuistriata	*Abies firma*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Habroloma griseonigrum	*Quercus serrata, Quercus acutissima, Quercus acuta, Quercus glauca*	*folivore*	*n*	*m*
Coleoptera	Buprestidae	Lamprodila virgata	*Quercus crispula*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Melanophila obscurata	*Abies firma, Abies sachalinensis, Larix kaempferi*	*wood*	*y*	*m*
Coleoptera	Buprestidae	Nalanda chinensis	*Quercus variabilis, Quercus serrata*	*wood*	*n*	*m*
Coleoptera	Buprestidae	Nalanda primoriensis	*Salix gracilistyla*	*wood*	*n*	*l*
Coleoptera	Buprestidae	Nipponobuprestis amabilis	*Prunus × yedoensis*	*folivore*	*n*	*l*
Coleoptera	Buprestidae	Toxoscelus auriceps	*Quercus serrata,Quercus aliena*	*wood*	*n*	*l*
Coleoptera	Buprestidae	Trachys inconspicuus	*Prunus mume*	*folivore*	*n*	*l*
Coleoptera	Buprestidae	Trachys minutus subsp. salicis	*Populus suaveolens,*	*folivore*	*n*	*h*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Coleoptera	Buprestidae	Trachys toringoi	*Malus toringo*	*folivore*	*n*	*l*
Coleoptera	Buprestidae	Trachys variolaris	*Quercus glauca, Quercus serrata, Quercus crispula, Quercus dentata, Quercus acutissima, Quercus variabilis*	*folivore*	*n*	*m*
Coleoptera	Cerambycidae	Anoplophora chinensis	*Populus pseudoglauca, Populus cathayana, Populus pseudosimonii, Populus simonii, Populus suaveolens*	*wood*	*n*	*l*
Coleoptera	Cerambycidae	Anoplophora glabripennis	*Acer buergerianum, Acer pictum, Acer truncatum, Salix babylonica, Populus simonii, Populus cathayana, Populus pseudoglauca*	*wood*	*n*	*l*
Coleoptera	Cerambycidae	Aromia bungii	*Prunus persica, Prunus grayana, Prunus yedoensis, Prunus japonica*	*wood*	*n*	*l*
Coleoptera	Cerambycidae	Batocera davidis	*Pinus massoniana, Malus pumila*	*wood*	*n*	*l*
Coleoptera	Cerambycidae	Batocera horsfieldi	*Fraxinus chinensis, Populus tomentosa*	*wood*	*n*	*l*
Coleoptera	Cerambycidae	Callidiellum rufipenne	*Thuja* spp., *Juniperus* spp., *Chamaecyparis obtusa*	wood	n	m
Coleoptera	Cerambycidae	Coscinesthes salicis	*Populus alba*	*wood*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Coleoptera	Cerambycidae	Mesosa myops	*Quercus mongolica, Quercus wutaishanica, Fraxinus mandshurica*	*wood*	*n*	*m*
Coleoptera	Cerambycidae	Monochamus alternatus	*Abies firma, Pinus armandii, Pinus massoniana, Pinus yunnanensis, Pinus densiflora*	*wood*	*n*	*m*
Coleoptera	Cerambycidae	Purpuricenus sideriger	*Quercus chenii, Quercus glauca*	*wood*	*n*	*m*
Coleoptera	Cerambycidae	Semanotus bifasciatus	*Thuja spp., Juniperus spp., Chamaecyparis spp.*	*wood*	*y*	*m*
Coleoptera	Cerambycidae	Stromatium longicorne	*Picea spp., Pinus spp., Populus spp., Quercus spp.*	*wood*	*n*	*h*
Coleoptera	Chrysomelidae	Adiscus lewisii	*Quercus acutissima, Quercus serrata*	*Folivore*	*n*	*m*
Coleoptera	Chrysomelidae	Agelastica coerulea	*Alnus japonica, Alnus hirsuta, Betula platyphylla*	*Folivore*	*n*	*m*
Coleoptera	Chrysomelidae	Aphthona perminuta	*Quercus serrata*	*Folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Argopistes biplagiatus	*Fraxinus japonica*	*Folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Arthrotus niger	*Acer pictum, Alnus japonica*	*Folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Basilepta balyi	*Alnus japonica*	*Folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Basilepta pallidula	*Pinus densiflora, Pinus thunbergii*	*Folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Chlamisus consimilis	*Quercus dentata*	*Folivore*	*n*	*m*
Coleoptera	Chrysomelidae	Chlamisus spilotus	*Quercus serrata*	*Folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Cleoporus variabilis	*Prunus mume*	*Folivore*	*n*	*l*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Coleoptera	Chrysomelidae	Coenobius sulcicollis	*Quercus serrata*	*Folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Colaspoides japanus	*Quercus acutissima*	*Folivore*	*n*	*m*
Coleoptera	Chrysomelidae	Cryptocephalus aeneoblitus	*Quercus serrata*	*Folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Cryptocephalus amiculus	*Quercus serrata*	*Folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Cryptocephalus approximatus	*Quercus serrata, Populus Maximowiczii,*	*Folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Cryptocephalus confusus	*Quercus serrata, Alnus firma, Quercus acutissima*	*Folivore*	*n*	*m*
Coleoptera	Chrysomelidae	Cryptocephalus fortunatus	*Quercus acutissima*	*Folivore*	*n*	*m*
Coleoptera	Chrysomelidae	Cryptocephalus japanus	*Quercus dentata, Quercus acutissima, Quercus crispula, Quercus mongolica, Quercus serrata*	*Folivore*	*n*	*m*
Coleoptera	Chrysomelidae	Cryptocephalus luridipennis	*Alnus japonica, Malus sieboldii,*	*Folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Cryptocephalus nobilis	*Quercus dentata, Prunus grayana*	*Folivore*	*n*	*m*
Coleoptera	Chrysomelidae	Cryptocephalus perelegans	*Quercus serrata*	*Folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Cryptocephalus scitulus	*Quercus acutissima*	*Folivore*	*n*	*m*
Coleoptera	Chrysomelidae	Dactylispa subquadrata	*Quercus acutissima, Quercus glauca, Quercus mongolica, Quercus serrata, Quercus variabilis*	*Folivore*	*n*	*m*
Coleoptera	Chrysomelidae	Demotina fasciata	*Quercus dentata*	*Folivore*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Coleoptera	Chrysomelidae	Fidia atra	*Prunus mume*	*root*	*n*	*l*
Coleoptera	Chrysomelidae	Fidia kiiensis	*Quercus dentata*	*root*	*n*	*m*
Coleoptera	Chrysomelidae	Gastrolina peltoidea	*Alnus hirsuta*	*folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Gonioctena japonica	*Alnus japonica*	*folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Gonioctena morimotoi	*Prunus grayana, Prunus yedoensis, Prunus buergeriana*	*folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Gonioctena sibirica	*Populus suaveolens*	*folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Gonioctena springlovae	*Populus suaveolens*	*folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Hesperomorpha hirsuta	*Alnus hirsuta*	*folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Liroetis coeruleipennis	*Quercus acutissima*	*folivore*	*n*	*m*
Coleoptera	Chrysomelidae	Phratora grandis	*Salix reinii*	*folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Pyrrhalta fuscipennis	*Acer pictum*	*folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Smaragdina nipponensis	*Quercus acutissima, Quercus serrata*	*folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Thlaspida lewisii	*Fraxinus lanuginosa*	*folivore*	*n*	*l*
Coleoptera	Chrysomelidae	Trichochrysea okinawana	*Quercus acutissima*	*folivore*	*n*	*m*
Coleoptera	Curculionidae	Dendroctonus armandi	*Pinus armandii, Pinus tabulaeformis, Pseudotsuga sinensis*	*wood*	*y*	*m*
Coleoptera	Curculionidae	Dinorhopala takahashii	*Prunus jamasakura, Prunus salicina*	*foliage*	*n*	*l*
Coleoptera	Curculionidae	Ips hauseri	*Picea schrenkiana, Larix siberica*	*wood*	*y*	*m*
Coleoptera	Curculionidae	Ips nitidus	*Picea crassifolia, Pinus spp.*	*wood*	*y*	*l*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Coleoptera	Curculionidae	Ips shangrila	*Picea crassifolia*	*wood*	*y*	*l*
Coleoptera	Curculionidae	Ips subelongatus	*Larix sibirica, Larix gmelinii, Larix leptolepis, Larix kaempferi, Larix siberica, Pinus koraiensis*	*wood*	*y*	*m*
Coleoptera	Curculionidae	Rhamphus hisamatsui	*Acer mono, Alunus firma, Alnus japonica, Betula ermanii, Betula platyphylla*	*folivore*	*n*	*m*
Coleoptera	Curculionidae	Rhynchaenus japonicus	*Quercus acutissima, Quercus serrata and Quercus dentata*	*folivore*	*n*	*m*
Coleoptera	Curculionidae	Sipalinus gigas	Pinus massoniana, Pinus koraiensis, Pinus tabulaeformis	wood	n	l
Coleoptera	Vesperidae	Philus antennatus	*Pinus spp.*	*root*	*n*	*l*
Diptera	Cecidomyiidae	Cecidomyia yunnanensis	*Pinus yunnanensis*	*gall*	*n*	*l*
Hemiptera	Adelgidae	Adelges glandulae	*Picea brechytyla, Picea likiangensis, Abies fabri*	*sap*	*y*	*m*
Hemiptera	Adelgidae	Pineus cembrae pinikoreanus	*Pinus koraiensis, Picea jezoensis*	*sap*	*y*	*l*
Hemiptera	Adelgidae	Pineus cladogenous	*Pinus koraiensis*	*sap*	*y*	*l*
Hemiptera	Adelgidae	Pineus cortecicolus	*Pinus koraiensis*	*sap*	*y*	*l*
Hemiptera	Adelgidae	Pineus sichuananus	*Picea purpurea, Picea likiangensis*	*sap*	*y*	*m*
Hemiptera	Aphididae	Cinara pinitabulaeformis	*Pinus tabuliformis, Pinus massoniana, Pinus densiflora, Pinus luchuensis*	*sap*	*y*	*l*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Hemiptera	Aphididae	Lachnus tropicalis	*Quercus*	*sap*	*n*	*l*
Hemiptera	Aphididae	Prociphilus oriens	*Fraxinus mandshurica, Fraxinus platypoda, Fraxinus chinensis, Fraxinus sieboldiana*	*sap*	*y*	*l*
Hemiptera	Aphrophoridae	Aphrophora flavipes	*Pinus thunbergii, Pinus densiflora, Pinus tabulaeformis*	*sap*	*n*	*l*
Hemiptera	Cicadidae	Cryptotympana atrata	*Salix babylonica, Populus tomentosa, Prunus serrulata,*	*sap*	*n*	*l*
Hemiptera	Coccidae	Ceroplastes japonicus	*Quercus acutissima, Acer japonicum, Salix chaenomeloides, Salix sieboldiana, Prunus serrulata*	*sap*	*y*	*m*
Hemiptera	Coccidae	Ericerus pela	*Fraxinus bungeana, Fraxinus chinensis, Fraxinus longicuspis, Fraxinus mandshurica*	*sap*	*n*	*l*
Hemiptera	Coccidae	Eulecanium kuwanai	*Salix babylonica*	*sap*	*n*	*l*
Hemiptera	Coccidae	Parthenolecanium orientale	*prunus, salix*	*sap*	*n*	*l*
Hemiptera	Coreidae	Gonocerus yunnanensis	*Pinus yunnanensis, Pinus massoniana*	*sap*	*n*	*l*
Hemiptera	Diaspididae	Hemiberlesia pitysophila	*Pinus massoniana*	*sap*	*n*	*l*
Hemiptera	Diaspididae	Lepidosaphes salicina	*Betula platyphylla, Fraxinus spp., Salix spp.*	*sap*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Hemiptera	Diaspididae	Pseudaonidia duplex	*Quercus phillyreoides, Alnus hirsuta, Acer palmatum*	*sap*	*n*	*m*
Hemiptera	Diaspididae	Shansiaspis sinensis	*Salix matsudana*	*sap*	*n*	*l*
Hemiptera	Eriococcidae	Acanthococcus salicis	*Salix babylonica*	*sap*	*n*	*l*
Hemiptera	Eriococcidae	Asiacornococcus kaki	*Prunus armeniaca*	*sap*	*n*	*l*
Hemiptera	Kermesidae	Kermes miyasakii	*Quercus acutissima, Quercus aliena, Quercus serrata, Quercus variabilis*	*sap*	*y*	*m*
Hemiptera	Kermesidae	Kermes nawae	*Quercus acutissima, Quercus serrata*	*sap*	*y*	*m*
Hemiptera	Kermesidae	Kermes taishanensis	*Quercus acutissima, Quercus variabilis*	*sap*	*y*	*m*
Hemiptera	Kermesidae	Nidularia japonica	*Quercus acutissima, Quercus aliena, Quercus dentata, Quercus fabrei, Quercus serrata,*	*sap*	*n*	*m*
Hemiptera	Matsucoccidae	Matsucoccus dahuriensis	*Pinus sylvestris var. mongolica*	*sap*	*n*	*l*
Hemiptera	Matsucoccidae	Matsucoccus koraiensis	*Pinus koraiensis*	*sap*	*n*	*l*
Hemiptera	Matsucoccidae	Matsucoccus massonianae	*Larix kaempferi, Pinus massoniana, Pinus thunbergii*	*sap*	*y*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Hemiptera	Matsucoccidae	Matsucoccus matsumurae	*Pinus densiflora, Pinus kesiya, Pinus koraiensis, Pinus luchuensis, Pinus pumila, Pinus taiwanensis, Pinus tabulaeformis, Pinus massoniana, Pinus thunbergii*	*sap*	*y*	*l*
Hemiptera	Matsucoccidae	Matsucoccus sinensis	*Pinus densata, Pinus massoniana, Pinus tabuliformis, Pinus thunbergii, Pinus yunnanensis*	*sap*	*y*	*l*
Hemiptera	Matsucoccidae	Matsucoccus yunnanensis	*Pinus yunnanensis*	*sap*	*y*	*l*
Hemiptera	Monophlebidae	Drosicha corpulenta	*Quercus acuta, Quercus dentata, Quercus mongolica, Quercus serrata, Acer barbinerve, Acer pictum, Malus prunifolia, Prunus persica*	*sap*	*n*	*m*
Hemiptera	Pseudococcidae	Phenacoccus fraxinus	*Fraxinus chinensis*	*sap*	*n*	*l*
Hemiptera	Tingidae	Uhlerites debilis	*Quercus acutissima, Quercus dentata, Quercus phillyreoides, Quercus serrata*	*sap*	*n*	*l*
Hemiptera	Urostylididae	Urostylis westwoodii	*Quercus acutissima, Quecrus serrata*	*sap*	*n*	*m*
Hymenoptera	Diprionidae	Diprion hani	*Pinus koraiensis*	*folivore*	*n*	*l*
Hymenoptera	Diprionidae	Diprion jingyuanensis	*Pinus tabulaeformis*	*folivore*	*n*	*l*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Hymenoptera	Diprionidae	Diprion koreanus	*Larix gmelinii, Larix kaempferi*	*folivore*	*n*	*m*
Hymenoptera	Diprionidae	Diprion liuwanensis	*Pinus massionia, Pinus hwangshanensis*	*folivore*	*n*	*l*
Hymenoptera	Diprionidae	Diprion nanhuaensis	*Pinus yunnanensis, Pinus kesiya*	*folivore*	*n*	*l*
Hymenoptera	Diprionidae	Diprion nipponicus	*Pinus densiflora, Larix kaempferi*	*folivore*	*n*	*m*
Hymenoptera	Diprionidae	Gilpinia tohi	*Picea jezoensis, Picea glehnii*	*folivore*	*n*	*l*
Hymenoptera	Diprionidae	Neodiprion dailingensis	*Pinus tubulueformis, Pinus koraiensis*	*folivore*	*y*	*l*
Hymenoptera	Diprionidae	Neodiprion fengningensis	*Picea crassifolia*	*folivore*	*y*	*l*
Hymenoptera	Diprionidae	Neodiprion guangxiicus	*pinus yunnanensis*	*folivore*	*y*	*l*
Hymenoptera	Diprionidae	Neodiprion xiangyunicus	*pinus yunnanensis*	*folivore*	*y*	*l*
Hymenoptera	Diprionidae	Nesodiprion huanglongshanicus	*Pinus tabuliformis, Pinus armandii*	*folivore*	*n*	*l*
Hymenoptera	Diprionidae	Nesodiprion japonicus	*Pinus thunbergii, Larix kaempferi, Pinus densiflora, Pinus koraiensis, Pinus massoniana, Pinus thunbergii, Pinus wallichiana*	*folivore*	*n*	*m*
Hymenoptera	Diprionidae	Nesodiprion zhejiangensis	*Pinus massoniana, Pinus elliottii, Pinus thunbergia and Pinus taeda*	*folivore*	*n*	*l*
Hymenoptera	Pamphiliidae	Acantholyda flavalbimarginata	*Pinus yunnanensis*	*folivore*	*y*	*l*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Hymenoptera	Pamphiliidae	Cephalcia isshikii	*Picea jezoensis, Picea glehnii*	*folivore*	*n*	*l*
Hymenoptera	Pamphiliidae	Cephalcia variegata	*Pinus pumila*	*folivore*	*y*	*l*
Hymenoptera	Tenthredinidae	Anafenusa acericola	*Acer truncatum*	*folivore*	*n*	*l*
Hymenoptera	Tenthredinidae	Anoplonyx orientis	*Larix kaempferi*	*folivore*	*y*	*m*
Hymenoptera	Tenthredinidae	Craesus betulae	*Betula utilis*	*folivore*	*n*	*h*
Hymenoptera	Tenthredinidae	Euura itoi	*Larix kaempferi*	*gall*	*n*	*m*
Hymenoptera	Tenthredinidae	Macrophya fraxina	*Fraxinus chinensis*	*folivore*	*n*	*l*
Hymenoptera	Tenthredinidae	Macrophya satoi	*Fraxinus japonica*	*folivore*	*n*	*l*
Hymenoptera	Tenthredinidae	Messa taianensis	*Populus simonii, Populus yunnanensis*	*folivore*	*n*	*l*
Hymenoptera	Tenthredinidae	Nematus hequensis	*populus alba, Salix babylonica, Salix gordejevii*	*folivore*	*n*	*m*
Hymenoptera	Tenthredinidae	Pristiphora brevitheca	*Picea meyeri*	*folivore*	*n*	*l*
Hymenoptera	Tenthredinidae	Pristiphora ezomatsuvora	*Picea glehnii, Picea koyamae, Picea jezoensis, Picea shirasawae*	*folivore*	*n*	*l*
Hymenoptera	Tenthredinidae	Pristiphora huangi	*Prunus persica*	*folivore*	*n*	*l*
Lepidoptera	Adelidae	Nemophora raddei	*Salix sieboldiana*	*flowers*	*n*	*l*
Lepidoptera	Argyresthiidae	Argyresthia fujiyamae	*Larix kaempferi*	*folivore*	*y*	*m*
Lepidoptera	Argyresthiidae	Argyresthia nemorivaga	*Abies sachalinensis*	*folivore*	*n*	*m*
Lepidoptera	Autostichinae	Autosticha truncicola	*Prunus mume*	*folivore*	*n*	*l*
Lepidoptera	Blastobasidae	Blastobasis sprotundalis	*Quercus crispula*	*folivore*	*n*	*m*
Lepidoptera	Blastobasidae	Holcocera sakura	*Prunus × yedoensis*	*fruit*	*n*	*l*
Lepidoptera	Blastobasidae	Neoblastobasis biceratala	*Quercus serrata, Quercus crispula*	*fruit*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Bucculatricidae	Bucculatrix comporabile	*Quercus dentata, Quercus crispula, Quercus serrata*	*Folivore*	*y*	*m*
Lepidoptera	Bucculatricidae	Bucculatrix muraseae	*Alnus japonica*	*Folivore*	*n*	*l*
Lepidoptera	Bucculatricidae	Bucculatrix tsurubamella	*Quercus acutissima*	*Folivore*	*y*	*m*
Lepidoptera	Coleophoridae	Coleophora hancola	*Alnus japonica, Alnus hirsuta, Alnus inokumae*	*Folivore*	*n*	*l*
Lepidoptera	Coleophoridae	Coleophora levantis	*Quercus crispula, Quercus serrata, Quercus dentata, Quercus mongolica*	*Folivore*	*n*	*m*
Lepidoptera	Coleophoridae	Coleophora melanograpta	*Quercus dentata, Quercus acutissima, Quercus crispula*	*Folivore*	*n*	*m*
Lepidoptera	Coleophoridae	Coleophora obducta	*Larix kaempferi, Larix gmelinii*	*Folivore*	*n*	*m*
Lepidoptera	Coleophoridae	Coleophora platyphyllae	*Betula platyphylla, Betula ermanii, Betula maximowicziana*	*Folivore*	*n*	*m*
Lepidoptera	Coleophoridae	Coleophora quercicola	*Quercus crispula, Quercus acutissima, Quercus mongolica*	*Folivore*	*n*	*m*
Lepidoptera	Coleophoridae	Coleophora sakurae	*Prunus grayana, Prunus × yedoensis*	*Folivore*	*n*	*l*
Lepidoptera	Cosmopterigidae	Labdia citracma	*Quercus acutissima*	*wood*	*n*	*m*
Lepidoptera	Depressariidae	Agonopterix lacteella	*Fraxinus mandshurica*	*Folivore*	*n*	*l*
Lepidoptera	Depressariidae	Depressaria irregularis	*Quercus serrata, Quercus crispula*	*Folivore*	*n*	*m*
Lepidoptera	Depressariidae	Depressaria taciturna	*Quercus crispula*	*Folivore*	*n*	*m*
Lepidoptera	Epimarptidae	Epimarptis hiranoi	*Quercus serrata*	*Folivore*	*n*	*l*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Erebidae	Calliteara axutha	*Pinus massoniana, Pinus merkusii*	*Folivore*	*n*	*l*
Lepidoptera	Erebidae	Euproctis subflava	*Quercus serrata, Quercus variabilis, Quercus cerris, Quercus acutissima*	*Folivore*	*n*	*m*
Lepidoptera	Erebidae	Leucoma candida	*Populus seiboldii, Malus tschonoskii*	*Folivore*	*n*	*l*
Lepidoptera	Erebidae	Lymantria dispar spp. asiatica	*Quercus spp., Larix spp., Betula spp,. Salix spp., Juniperus spp.*	*Folivore*	*n*	*m*
Lepidoptera	Erebidae	Lymantria dissoluta	*Pinus massoniana, Pinus tabulaeformis, Pinus thunbergii, Quercus spp.*	*Folivore*	*n*	*l*
Lepidoptera	Erebidae	Lymantria fumida	*Abies firma*	*Folivore*	*n*	*m*
Lepidoptera	Erebidae	Lymantria mathura	*Quercus serrata, Quercus acuta, Quercus dentata*	*Folivore*	*n*	*m*
Lepidoptera	Eriocraniidae	Eriocrania sakhalinella	*Alnus hirsuta, Alnus japonica*	*Folivore*	*n*	*l*
Lepidoptera	Gelechiidae	Agnippe syrictis	*Prunus mume*	*Folivore*	*n*	*l*
Lepidoptera	Gelechiidae	Altenia inscriptella	*Acer tataricum*	*Folivore*	*n*	*l*
Lepidoptera	Gelechiidae	Anacampsis triangulella	*Betula platyphylla*	*Folivore*	*n*	*m*
Lepidoptera	Gelechiidae	Anarsia patulella	*Prunus salicina*	*reproducive*	*n*	*l*
Lepidoptera	Gelechiidae	Chorivalva bisaccula	*Quercus acutissima, Quercus serrata*	*Folivore*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Gelechiidae	Dichomeris heriguronis	*Prunus mume*	*Folivore*	*n*	*l*
Lepidoptera	Gelechiidae	Dichomeris tostella	*Prunus mume*	*Folivore*	*n*	*l*
Lepidoptera	Gelechiidae	Faristenia acerella	*Acer tataricum*	*Folivore*	*n*	*l*
Lepidoptera	Gelechiidae	Faristenia geminisignella	*Acer pictum*	*Folivore*	*n*	*l*
Lepidoptera	Gelechiidae	Gelechia anomorcta	*Quercus crispula*	*Folivore*	*n*	*m*
Lepidoptera	Gelechiidae	Gelechia inconspicua	*Salix gilgiana*	*Folivore*	*n*	*l*
Lepidoptera	Gelechiidae	Gelechia teleiodella	*Quercus mongolica, Abies sachalinensis*	*Folivore*	*n*	*m*
Lepidoptera	Gelechiidae	Psoricoptera arenicolor	*Betula ermanii*	*Folivore*	*n*	*m*
Lepidoptera	Gelechiidae	Stenolechia kodamai	*Pinus densiflora*	*Folivore*	*n*	*l*
Lepidoptera	Gelechiidae	Stenolechia notomochla	*Quercus dentata*	*Folivore*	*n*	*m*
Lepidoptera	Gelechiidae	Thiotricha fusca	*Alnus japonica, Alnus hirsuta*	*Folivore*	*n*	*l*
Lepidoptera	Gelechiidae	Thiotricha relictana	*Betula ermanii, Betula grossa*	*Folivore*	*n*	*m*
Lepidoptera	Gelechiidae	Thiotricha synodonta	*Betula platyphylla, Betula ermanii, Alnus hirsuta*	*Folivore*	*n*	*m*
Lepidoptera	Geometridae	Abraxas flavisinuata	*Pinus massoniana, Pinus yunnanensis*	*Folivore*	*n*	*l*
Lepidoptera	Geometridae	Apocheima cinerarius	*Populus euphratica, Malus pumila*	*Folivore*	*n*	*l*
Lepidoptera	Geometridae	Biston suppressaria	*Prunus salicina, although tea (Camillia sinensis) is prefered host*	*Folivore*	*n*	*l*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Geometridae	Larerannis filipjevi	*Prunus salicina, Prunus sargentii, Quercus mongolica, Populus tremula, Fraxinus mandshurica*	*Folivore*	*n*	*m*
Lepidoptera	Geometridae	Larerannis orthogrammaria	*Betula utilis, Betula platyphylla, Betula mandshurica, Betula albosinensis*	*Folivore*	*n*	*hm*
Lepidoptera	Geometridae	Meichihuo cihuai	*Prunus yedoensis, Prunus serrulata, Acer palmatum, Acer pseudosieboldianum*	*Folivore*	*n*	*m*
Lepidoptera	Geometridae	Xerodes rufescentaria	*Abies sachalinensis, Larix kaempferi*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Acrocercops querci	*Quercus glauca*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Acrocercops unistriata	*Quercus acuta, Quercus glauca*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Acrocercops vallata	*Quercus acuta, Quercus glauca,Quercus salicina*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Caloptilia acericola	*Acer japonicum, Acer palmatum, Acer tataricum, Acer pictum*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Caloptilia aceris	*Acer miyabei, Acer pictum*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Caloptilia alni	*Alnus hirsuta*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Caloptilia chrysolampra	*Populus tremula, Salix babylonica*	*Folivore*	*n*	*l*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Gracillariidae	Caloptilia gloriosa	*Acer japonicum, Acer sieboldianum*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Caloptilia heringi	*Acer pictum*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Caloptilia hidakensis	*Acer pictum*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Caloptilia issikii	*Alnus japonica*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Caloptilia kurokoi	*Acer argutum, Acer distylum*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Caloptilia mandschurica	*Castanea crenata, Quercus acutissima, Quercus crispula, Quercus dentata, Quercus mongolica, Quercus serrata*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Caloptilia monticola	*Acer argutum, Acer distylum*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Caloptilia obliquatella	*Quercus acutissima*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Caloptilia pulverea	*Alnus firma, Alnus japonica*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Caloptilia pyrrhaspis	*Betula ermanii, Betula grossa*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Caloptilia querci	*Quercus acutissima*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Caloptilia sapporella	*Quercus acutissima, Quercus crispula*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Caloptilia semifasciella	*Acer rufinerve, Acer tschonoskii*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Caloptilia wakayamensis	*Acer palmatum, Acer shirasawanum*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Caloptilia yasudai	*Acer pictum*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Cameraria acericola	*Acer pictum*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Cameraria niphonica	*Acer palmatum, Acer japonicum*	*Folivore*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Gracillariidae	Cryptolectica chrysalis	*Quercus crispula, Quercus serrata*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Cryptolectica ensiformis	*Quercus acuta, Quercus sessilifolia*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Dendrorycter marmaroides	*Alnus hirsuta*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Gracillaria albicapitata	*Fraxinus mandshurica*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Gracillaria arsenievi	*Fraxinus mandshurica*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Gracillaria ussuriella	*Fraxinus mandshurica*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Metriochroa fraxinella	*Fraxinus sieboldiana*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Parornix alni	*Alnus hirsuta*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Parornix multimaculata	*Malus baccata, Prunus avium, Prunus maximowiczii, Prunus mume, Prunus sachalinensis, Prunus salicina, Prunus sargentii*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Phyllocnistis cornella	Cornus controversa	*Folivore*	n	l
Lepidoptera	Gracillariidae	Phyllocnistis gracilistylella	*Salix gracilistyla, Salix integra*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Phyllocnistis indistincta	Cornus macrophylla, Cornus kousa, Cornus controversa	*Folivore*	n	m
Lepidoptera	Gracillariidae	Phyllocnistis saepta	Cornus macrophylla	*Folivore*	n	l
Lepidoptera	Gracillariidae	Phyllocnistis verae	Cornus alba	*Folivore*	n	l
Lepidoptera	Gracillariidae	Phyllonorycter acutissimae	*Quercus acutissima, Quercus variabilis, Quercus crispula*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter cretata	*Quercus crispula, Quercus serrata*	*Folivore*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Gracillariidae	Phyllonorycter dakekanbae	*Betula ermanii*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter ermani	*Betula ermanii*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter ginnalae	*Acer tataricum*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Phyllonorycter hancola	*Alnus japonica, Alnus hirsuta*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Phyllonorycter jezoniella	*Acer pictum*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Phyllonorycter jozanae	*Crataegus chlorosarca*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Phyllonorycter kamijoi	*Quercus acutissima*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter kisoensis	*Alnus hirsuta*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Phyllonorycter kurokoi	*Acer pictum*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Phyllonorycter leucocorona	*Quercus dentata, Quercus serrata*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter longispinata	*Alnus japonica, Alnus hirsuta*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Phyllonorycter maculata	*Alnus hirsuta*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Phyllonorycter matsudai	*Quercus crispula*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter mongolicae	*Quercus crispula, Quercus serrata, Quercus mongolica*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter nigristella	*Quercus crispula, Quercus serrata, Quercus mongolica*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter nipponicella	*Quercus acutissima, Quercus variabilis*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter orientalis	*Acer pictum, Acer palmatum, Acer mono, Acer carpinifolium*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter persimilis	*Quercus dentata*	*Folivore*	*n*	*l*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Gracillariidae	Phyllonorycter pseudolautella	*Quercus crispula, Quercus serrata, Quercus mongolica*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter pygmaea	*Quercus crispula, Quercus serrata, Quercus mongolica, Quercus acutissima, Quercus crenata*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter ringoniella	*Malus toringo, Malus baccata, Prunus salicina*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Phyllonorycter rostrispinosa	*Quercus acutissima, Quercus crispula, Quercus serrata*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter similis	*Quercus crispula, Quercus serrata, Quercus acutissima, Quercus cerris, Quercus dentata, Quercus mongolica*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Phyllonorycter takagii	*Alnus japonica*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Spulerina astaurota	*Malus toringo*	*Folivore*	*n*	*l*
Lepidoptera	Gracillariidae	Spulerina castaneae	*Quercus crispula*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Spulerina corticicola	*Abies sachalinensis, Larix kaempferi, Pinus parviflora*	*Folivore*	*n*	*m*
Lepidoptera	Gracillariidae	Spulerina virgulata	*Quercus acutissima Quercus serrata, Quercus variabilis*	*Folivore*	*n*	*m*
Lepidoptera	Hepialidae	Endoclita excrescens	*Quercus acutissima*	*wood*	*n*	*m*
Lepidoptera	Hepialidae	Endoclita sinensis	*Quercus acutissima*	*wood*	*n*	*m*
Lepidoptera	Incurvariidae	Incurvaria alniella	*Alnus japonica*	*Folivore*	*n*	*l*
Lepidoptera	Incurvariidae	Paraclemensia cyanea	*Betula platyphylla*	*Folivore*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Incurvariidae	Vespina nielseni	*Quercus aliena, Quercus acutissima, Quercus serrata*	*Folivore*	*n*	*m*
Lepidoptera	Lasiocampidae	Dendrolimus kikuchii	*Pinus massoniana, Pinus latteri*	*Folivore*	*n*	*l*
Lepidoptera	Lasiocampidae	Dendrolimus punctatus	*Pinus parviflora, Pinus thunbergii, Pinus massoniana, Pinus armandii, Pinus tabulaeformis*	*Folivore*	*n*	*l*
Lepidoptera	Lasiocampidae	Dendrolimus spectabilis	*Pinus densiflora, Pinus thunbergii, Pinus tabulaeformis*	*Folivore*	*n*	*l*
Lepidoptera	Lasiocampidae	Dendrolimus superans	*Tsuga sieboldii, Larix gmelinii, Larix kaempferi, Pinus pumila, Abies sachalinensis, Picea jezoensis, Pinus koraiensis,Pinus thunbergii*	*Folivore*	*n*	*m*
Lepidoptera	Lasiocampidae	Dendrolimus tabulaeformis	*Pinus tabulaeformis*	*Folivore*	*n*	*l*
Lepidoptera	Lasiocampidae	Kunugia latipennis	*Pinus kesiya*	*Folivore*	*n*	*l*
Lepidoptera	Limacodidae	Ceratonema sericeum	*Acer palmatum*	*Folivore*	*n*	*m*
Lepidoptera	Limacodidae	Kitanola uncula	*Alnus matsumurae, Acer palmatum*	*Folivore*	*n*	*m*
Lepidoptera	Limacodidae	Quasinarosa edoensis	*Prunus mume*	*Folivore*	*n*	*l*
Lepidoptera	Lyonetiidae	Leucoptera ermolaevi	*Acer tataricum*	*Folivore*	*n*	*l*
Lepidoptera	Lyonetiidae	Lyonetia bakuchia	*Prunus zippeliana*	*Folivore*	*n*	*l*
Lepidoptera	Lyonetiidae	Lyonetia castaneella	*Quercus acutissima*	*Folivore*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Lyonetiidae	Lyonetia kurokoi	*Betula platyphylla, Alnus japonica*	*Folivore*	*n*	*m*
Lepidoptera	Lyonetiidae	Lyonetia yasudai	*Quercus acuta, Prunus spinulosa, Prunus zippeliana*	*Folivore*	*n*	*l*
Lepidoptera	Lypusidae	Diurnea fumida	*Alnus japonica, Salix gracilistyla*	*Folivore*	*n*	*l*
Lepidoptera	Nepticulidae	Ectoedemia cerviparadisicola	*Quercus gilva*	*Folivore*	*n*	*m*
Lepidoptera	Nepticulidae	Ectoedemia chasanella	*Quercus dentata, Quercus crispula, Quercus serrata, Quercus acutissima*	*Folivore*	*n*	*m*
Lepidoptera	Nepticulidae	Ectoedemia insularis	*Salix gilgiana*	*Folivore*	*n*	*l*
Lepidoptera	Nepticulidae	Ectoedemia olvina	*Acer pictum, Acer palmatum*	*Folivore*	*n*	*m*
Lepidoptera	Nepticulidae	Stigmella aladina	*Quercus serrata, Quercus acutissima, Quercus dentata, Quercus mongolica*	*Folivore*	*n*	*m*
Lepidoptera	Nepticulidae	Stigmella alaurulenta	*Malus toringo*	*Folivore*	*n*	*l*
Lepidoptera	Nepticulidae	Stigmella azuminoensis	*Quercus serrata,Quercus acutissima, Quercus dentata*	*Folivore*	*n*	*m*
Lepidoptera	Nepticulidae	Stigmella azusa	*Salix dolichostyla, Salix serissaefolia*	*Folivore*	*n*	*l*
Lepidoptera	Nepticulidae	Stigmella caesurifasciella	*Quercus acuta, Quercus glauca*	*Folivore*	*n*	*m*
Lepidoptera	Nepticulidae	Stigmella clisiotophora	*Quercus variabilis*	*Folivore*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Nepticulidae	Stigmella dentatae	*Quercus dentata, Quercus serrata, Quercus crispula, Quercus mongolica*	*Folivore*	*n*	*m*
Lepidoptera	Nepticulidae	Stigmella fumida	*Quercus dentata, Quercus acutissima, Quercus variabilis*	*Folivore*	*n*	*m*
Lepidoptera	Nepticulidae	Stigmella hisakoae	*Quercus serrata*	*Folivore*	*n*	*l*
Lepidoptera	Nepticulidae	Stigmella kurokoi	*Quercus serrata, Quercus dentata, Quercus aliena*	*Folivore*	*n*	*m*
Lepidoptera	Nepticulidae	Stigmella monella	*Acer crataegifolium, Acer rufinerve, Acer pictum*	*Folivore*	*n*	*l*
Lepidoptera	Nepticulidae	Stigmella omelkoi	*Quercus serrata,Quercus dentata, Quercus crispula, Quercus mongolica*	*Folivore*	*n*	*m*
Lepidoptera	Nepticulidae	Stigmella tenryuensis	*Salix japonica*	*Folivore*	*n*	*l*
Lepidoptera	Nepticulidae	Stigmella titivillitia	*Alnus hirsuta, Alnus japonica*	*Folivore*	*n*	*l*
Lepidoptera	Nepticulidae	Stigmella ultima	*Acer pictum, Acer palmatum*	*Folivore*	*n*	*m*
Lepidoptera	Nepticulidae	Stigmella zumii	*Malus toringo*	*Folivore*	*n*	*l*
Lepidoptera	Notodontidae	Phalerodonta manleyi	*Quercus mongolica, Quercus acutissima, Quercus cerris, Quercus variabilis, Quercus serrata, Quercus glauca, Quercus aliena*	*Folivore*	*n*	*m*
Lepidoptera	Oecophoridae	Casmara agronoma	*Alnus firma, Alnus pendula, Alnus japonica*	*wood*	*n*	*l*
Lepidoptera	Oecophoridae	Promalactis jezonica	*Quercus crispula*	*wood*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Oecophoridae	Semnolocha pachysticta	*Prunus × yedoensis*	*Folivore*	*n*	*l*
Lepidoptera	Opostegidae	Opostegoides minodensis	*Betula platyphylla, Betula ermanii*	*wood*	*n*	*m*
Lepidoptera	Plutellidae	Rhigognostis japonica	*Abies sachalinensis*	*Folivore*	*n*	*m*
Lepidoptera	Praydidae	Prays alpha	*Fraxinus mandshurica*	*reproducive*	*n*	*l*
Lepidoptera	Praydidae	Prays beta	*Fraxinus japonica*	*reproducive*	*n*	*l*
Lepidoptera	Pyralidae	Cryptoblabes loxiella	*Larix kaempferi*	*Folivore*	*n*	*m*
Lepidoptera	Stathmopodidae	Oedematopoda beijingana	*Quercus acutissima, Quercus serrata*	*Folivore*	*n*	*m*
Lepidoptera	Stathmopodidae	Stathmopoda albiornata	*Quercus acutissima*	*reproducive*	*n*	*m*
Lepidoptera	Stathmopodidae	Stathmopoda flavescens	*Alnus japonica*	*reproducive*	*n*	*l*
Lepidoptera	Stathmopodidae	Stathmopoda moriutiella	*Abies sachalinensis*	*reproducive*	*n*	*m*
Lepidoptera	Tischeriidae	Manitischeria relictana	*Betula grossa, Betula ermanii*	*Folivore*	*n*	*m*
Lepidoptera	Tischeriidae	Tischeria naraensis	*Quercus acutissima, Quercus variabilis, Quercus acutissima, Quercus dentata, Quercus crispula*	*Folivore*	*n*	*m*
Lepidoptera	Tischeriidae	Tischeria quercifolia	*Quercus acutissima, Quercus crispula, Quercus dentata, Quercus serrata*	*Folivore*	*n*	*m*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Tortricidae	Acleris submaccana	*Betula platyphylla, Alnus maximowiczii, Alnus japonica, Duchesnea indica, Salix koreensis*	*Folivore*	*n*	*m*
Lepidoptera	Tortricidae	Choristoneura longicellanus	*Malus pumila, Quercus acutissima, Quercus aliena, Quercus dentata, Quercus mongolica, Quercus serrata, Quercus variabilis, Prunus persica, Prunus salicina, Prunus yedoensis*	*Folivore*	*n*	*m*
Lepidoptera	Tortricidae	Cydia glandicolana	*Quercus mongolica, Quercus dentate and Quercus serrata*	*reproducive*	*n*	*m*
Lepidoptera	Tortricidae	Retinia cristata	*Pinus thurnbergii, Pinus densiflora, Pinus massoniana, Pinus kesiya, Pinus koraiensis*	*Folivore*	*n*	*l*
Lepidoptera	Tortricidae	Retinia monopunctata	*Abies sachalinensis, Abies homolepis, Picea polita, Picea glehnii, Picea jezoensis, Abies holophylla, Pinus strobus, Larix kaempferi and Pinus koraiensis.*	*wood*	*n*	*m*
Lepidoptera	Tortricidae	Rhyacionia inslariana	*Pinus yunnanensis, Pinus densata, Pinus kesiya, Pinus armandi, Pinus massoniana.*	*Folivore*	*y*	*l*
Lepidoptera	Tortricidae	Saliciphaga caesia	*Salix rorida*	*wood*	*n*	*l*

Insect Order	Insect Family	Insect Genera (Species)	*Asian host*	*feeding guild*	*North American congener? y/n*	*risk rating*
Lepidoptera	Tortricidae	Spilonota eremitana	*Larix kaempferi*	*Folivore*	*n*	*m*
Lepidoptera	Xyloryctidae	Metathrinca tsugensis	*Picea jezoensis, Tsuga sieboldii*	*Folivore*	*n*	*l*
Lepidoptera	Yponomeutidae	Ocnerostoma friesei	*Pinus densiflora*	*Folivore*	*n*	*l*
Lepidoptera	Yponomeutidae	Thecobathra anas	*Quercus acutissima, Quercus serrata, Quercus glauca*	*Folivore*	*n*	*m*
Lepidoptera	Yponomeutidae	Yponomeuta orientalis	*Malus toringo, Malus baccata*	*Folivore*	*n*	*l*
Lepidoptera	Yponomeutidae	Yponomeuta polystictus	*Malus baccata*	*Folivore*	*n*	*l*
Lepidoptera	Yponomeutidae	Yponomeuta refrigerata	*Prunus ssiori*	*Folivore*	*n*	*l*
Lepidoptera	Yponomeutidae	Ypsolopha cristata	*Malus toringo*	*Folivore*	*n*	*l*
Lepidoptera	Yponomeutidae	Ypsolopha distinctata	*Quercus phillyraeoides*	*Folivore*	*y*	*m*
Lepidoptera	Yponomeutidae	Ypsolopha parallela	*Quercus serrata*	*Folivore*	*y*	*l*
Lepidoptera	Yponomeutidae	Ypsolopha tsugae	*Abies sachalinensis, Tsuga diversifolia*	*Folivore*	*n*	*m*

Appendix 2: Sources used for literature review

These sources on Asian insects were used to confirm names/synonyms, confirm native range, determine feeding guild, and determine host plants.

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