Tree Diversity and Forest Resistance to Insect Pests: Patterns, Mechanisms, and Prospects

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Abstract
Ecological research conducted over the past five decades has shown that increasing tree species richness at forest stands can improve tree resistance to insect pest damage. However, the commonality of this finding is still under debate. In this review, we provide a quantitative assessment (i.e., a meta-analysis) of tree diversity effects on insect herbivory and discuss plausible mechanisms underlying the observed patterns. We provide recommendations and working hypotheses that can serve to lay the groundwork for research to come. Based on more than 600 study cases, our quantitative review indicates that insect herbivory was, on average, lower in mixed forest stands than in pure stands, but these diversity effects were contingent on herbivore diet breadth and tree species composition. In particular, tree species diversity mainly reduced damage of specialist insect herbivores in mixed stands with phylogenetically distant tree species. Overall, our findings provide essential guidance for forest pest management.
1. INTRODUCTION

Forests are essential to meet the growing demand for biomaterials (104), to contribute to climate change mitigation (42), and to preserve biodiversity (98). However, natural threats such as fire, insect pests, and diseases are disrupting the flow of goods and services from forests. In particular, climate change is triggering large-scale outbreaks of forest insect pests through increasing temperatures, drought, and storms (63), while the number of invasions by non-native forest insect pests continues to increase worldwide (13), with a significant negative impact on forest functioning and economics (75). Pest management has historically relied on the use of agrochemicals, which generally are suited for short-term curative control. However, the adverse consequences of their widespread use have triggered severe environmental problems due to their persistence in the air, soil, water, and food, as well as the development of pest resistance (56). To reduce these risks, the European Union and the Forest Stewardship Council prescribe a reduction in the use of pesticides (e.g., neonicotinoids) (66) and give priority to the use of preventive, environmentally friendly methods of forest pest management.

Ecological research conducted over the past five decades has shown that plant species richness has substantial effects on ecosystem processes such as decomposition rates and productivity and can influence arthropod community structure and overall species richness at higher trophic levels (17, 126). In the case of plant–herbivore interactions, it has been commonly reported that the abundance or damage of insect pests is often lower in plant species mixtures than in monocultures (see Reference 9 and references therein). This observation has been termed associational resistance (121) and has been widely studied in agricultural (9, 87) and forestry (59, 61) systems. Two main mechanisms have been proposed to explain these associational resistance effects. First, the presence of heterospecific neighbors around a tree of a focal species grown in mixed stands leads to a lower probability of host tree finding by insect herbivores due to lower host abundance or frequency (resource concentration hypothesis) (121), to the confounding effect resulting from the mixing of cues emitted by host and nonhost trees (host apparency hypothesis) (23), or to preference for nonhost trees (decoy hypothesis) (6, 125). Second, heterospecific neighborhoods favor greater abundance of herbivore natural enemies (predators and parasitoids) because of increased availability of habitats or alternative resources, leading to reduced herbivore abundance and damage (121). However, more recently, and following the rise in tree diversity experiments (108), the commonly held view that tree species diversity leads to associational resistance has been questioned (69), with studies reporting neutral (47) or opposite (i.e., associational susceptibility) (22, 128, 147) patterns in mixed forest stands. In this sense, biodiversity–ecosystem functioning studies have greatly improved our understanding of physiological responses of focal trees to the identity and functional diversity of surrounding trees (113), particularly in terms of growth, energy allocation, and functional traits (112). A more complex vision of associational resistance effects is thus being proposed, involving, for example, the effects of tree diversity on tree traits involved in the attraction of herbivore natural enemies [e.g., volatile organic compounds (VOCs)] (3) or direct defense against herbivores (e.g., phenolic compounds) (22, 91). Finally, the ongoing recognition of the complexity of biotic interactions involving trees, including the exchange of matter and information between trees, between trees and the numerous microorganisms living inside trees, and between trees and some belowground organisms (e.g., mycorrhizae), is opening new avenues to understanding patterns of associational resistance or susceptibility.

In view of these uncertainties and the ongoing refinement of the mechanisms underpinning associational relationships in mixed forests, we provide a new quantitative assessment of tree species effects on insect herbivory by conducting a global meta-analysis of published studies involving more than 600 case studies in tropical, temperate, and boreal forests. We assess whether tree
diversity effects varied with respect to tree species composition, herbivore abundance, and herbivore diet breadth. We interpret results from this analysis in light of plausible mechanisms underlying observed patterns. Finally, we provide a perspective for future research on this topic. Overall, our objective is to reassess the current paradigm of forest diversity effects on tree–insect interactions and to indicate how this knowledge can be applied in practice to improve forest pest management.

2. META-ANALYSIS OF TREE SPECIES DIVERSITY EFFECTS ON INSECT HERBIVORY

We added literature to previous analyses (23, 61), which covered the period 1966–2012. We carried out an extensive literature search in the ISI Web of Knowledge database using the following search criteria: “(forest OR tree) AND (*diversity OR monoculture OR monospecific OR pure OR mix* OR polyculture) AND (pest OR herbivore* OR defoliation OR damage) AND insect.” We retained only articles, book chapters, reviews, theses, dissertations, and abstracts published in English. This search spanned published work from 2012 to 2019 and yielded 988 papers.

To be included in our meta-analyses, primary studies had to (a) report on the abundance or damage made by a given insect herbivore on the same tree species in both pure and mixed stands and (b) provide a measure of the treatment level means and variability (i.e., variance, standard error, or standard deviation), as well as the sample size, in the text, figures, tables, or appendices. When needed, we extracted data from figures following digitalization, using ImageJ 1.51j8 or WebPlotDigitizer software. After applying these criteria, the resulting data set consisted of $k = 624$ study cases (243 in boreal, 312 in temperate, and 71 in tropical forests) from $N = 69$ papers published between 1966 and 2019 in 43 scientific journals (see list of references in the Supplemental Appendix). For each study, we extracted a set of moderators to identify the mechanisms driving associational effects in forest ecosystems (see details in the Supplemental Appendix): study type (observational or experimental), local climatic conditions (obtained from the World-Clim database, based on geographical coordinates), proportion of focal tree in the mixture, type of mixture (angiosperms and/or gymnosperms), herbivore response type (e.g., abundance or damage), insect diet breadth (specialist versus generalist), insect species and feeding guild (e.g., chewer, borer, miner, sap feeder), and herbivory level (low versus high).

For each study case, we estimated effect sizes using the log ratio (LR) metric and its variance using the metafor package 1.9-8 version in R 3.2.3 (116, 143). LR was calculated as the standardized ratio between mean herbivory in tree mixture and in tree monocultures, such that negative values indicate associational resistance, whereas positive values indicate associational susceptibility.

We calculated a grand mean effect size across all studies to test the overall effect of tree species diversity on insect herbivores. This grand mean effect size was considered significant if its confidence interval (CI) did not overlap with zero (81). We estimated the level of consistency among studies by calculating between-study heterogeneity ($\tau^2$, associated $Q$ statistics) (81, 100). We ran preliminary analyses to evaluate the effects of study type (observational versus experimental), local climate (mean annual temperature and annual precipitation), herbivore response type (herbivore abundance versus damage), and herbivore feeding guild on the herbivory response to tree species diversity. Results of these analyses indicated that none of these moderators accounted for heterogeneity among studies (Supplemental Appendix). We therefore did not consider these moderators in further analyses. In a first step, we included all studies to estimate the grand mean effect size ($N = 69$ articles, $k = 624$ study cases). Then, in a second step, we included the proportion of focal trees, herbivore diet breadth, specific composition of mixed plot, and the two- and three-way interactions as moderators by using a subset limited to study cases in which the
herbivore species was clearly identified ($k = 318$); this allows us to be more careful in the documentation of the moderators and thus produce more conservative results.

The grand mean effect size ($±95\% \text{ CI}$) was significantly negative [$-0.23\% (-0.32\%; -0.13\%)$], showing that tree species growing in pure forests exhibited more damage by insect herbivores than the same species in mixed-species forests (i.e., associational resistance) (Figure 1a).

This result was consistent across herbivore feeding guilds (Figure 1b), study types (Figure 1c), and types of herbivore responses (Figure 1d). There was a significant amount of heterogeneity ($k = 624; \tau^2 = 0.39; Q_E = 25,645.89; P < 0.001$), of which 98% was due to between-study heterogeneity ($I^2 = 98.27$), indicating the necessity of using relevant moderators to model this heterogeneity.

A cumulative meta-analysis showed that the grand mean effect sizes were stable over time (Supplemental Appendix). Since 2000, there has been a tendency toward lower effect sizes, which, although they are significantly negative (associational resistance), might correspond to the increasing number of published papers from young tree diversity experiments (TreeDivNet) (43).
3. COMMON MECHANISMS UNDERLYING TREE SPECIES DIVERSITY EFFECTS ON HERBIVORY

3.1. Reduced Host Tree Abundance and Accessibility in Mixed Forests

Tree diversity effects on insect herbivores are primarily driven by the absolute (i.e., resource concentration) and relative (i.e., resource frequency) abundance of host trees that herbivores can perceive and access, which are determined by both the composition of forest stands and the diet breadth of insect herbivores. In our meta-analysis, we tested the effect of focal host tree frequency, mixed stand composition, and herbivore diet breadth on a subset of the complete data set corresponding to clearly identified herbivore species ($k = 318$). We found significant effects of the interactions between host frequency and herbivore diet breadth ($z = 2.31; P = 0.021$) and between herbivore diet breadth and the species composition of mixed stands ($z = 2.58, P = 0.010$). Specifically, the overall negative effect of tree diversity on insect herbivory strengthened with increasing dilution of the focal tree species among associated species (Figure 2a), but this effect was only significant for specialist herbivores [slope estimate for generalists: $-0.001 \pm (-0.010, 0.010)$; slope estimate for specialists: $0.013 \pm (0.006, 0.021)$]. Associational resistance was overall stronger and only significant in the case of specialist herbivores attacking a tree species associated with more phylogenetically distant species (i.e., mixtures of angiosperms and gymnosperms) (Figure 2b).

The resource concentration hypothesis (121, 124) predicts that specialist herbivores (i.e., those feeding on a single host species or few congeneric species) are more likely to immigrate into—and less likely to emigrate from—forest stands dominated by their host tree. This mechanism is
notably determined by herbivore ability to use visual (e.g., shape, color, variegation) and chemical (e.g., VOC) cues to identify and orientate toward their host trees (114, 144): The stronger is the intensity of the cues, the greater is the attraction. In addition, specialist insect herbivores are able to detect and avoid nonhost trees (139). For instance, conifer specialist woodborers were deterred by visual cues mimicking the white trunks of nonhost, broad-leaved tree species (14). Similarly, the release of nonhost chemicals has been shown to reduce infestation by stem borers (148) and leaf chews (60) in mixed conifer forests. Generalist herbivores, in contrast, are more flexible in their diet requirements and can successfully spill over onto and then exploit different host species (147) or even benefit from host diversity through diet mixing (85). Therefore, mixed forests may be perceived as homogeneous resource patches by generalist herbivores. Castagneyrol et al. (23) revisited the resource concentration hypothesis by accounting for the contribution of every associated tree species to the total amount of food resources available to generalist herbivores. Assuming a certain degree of phylogenetic conservatism in traits determining tree palatability and defenses (99), these authors proposed that the amount of resources available was reduced in mixed forest stands associated with phylogenetically distant species, thus resulting in associational resistance patterns even for generalist herbivores (23). Independent studies confirmed the interactive effect of plant species richness and phylogenetic diversity on insect herbivory (12, 31), whereby herbivore damage increased with plant species richness but only in cases of high genetic relatedness among associated plant species.

Further developments of the resource concentration hypothesis have stressed the importance of the relative frequency of host plants in species-rich plant communities (138), whereby both resource concentration and frequency independently and interactively determine herbivory levels on a given plant (11, 48, 79). For instance, an observational study found that the infestation rate by the Asian chestnut gall wasp, Dryocosmus kuriphilus, increased with the relative proportion of chestnuts (i.e., frequency), regardless of their concentration (in this case, tree density) (35). Vehviläinen et al. (141) also found evidence for associational resistance for silver birch trees (Betula pendula) when they grow with an increasing proportion of Scots pine trees in a stand. However, because host species concentration and frequency are generally confounded in mixed forests, their relative contributions to associational effects remain poorly understood.

The spatial scale at which host tree concentration influences insect herbivory, e.g., whole stand-level versus finer-scale local neighborhood, is crucial. It is expected that greater immigration of herbivores to stands where their resource is both abundant and frequent will lead to higher herbivore density in pure forests. However, it may also result in the dilution of attacks among individual trees when the number of trees far exceeds the number of insects attacking them (7, 105). For instance, in a tree diversity experiment in southwestern France, Damien et al. (29) found that the number of pine trees per stand attacked by the pine processionary moth, Thaumetopoea pityocampa, decreased with tree species richness (i.e., resource concentration effect), whereas the percentage of attacked trees increased (i.e., resource dilution effect). This result is consistent with the prediction that host tree infestation results from a sequential process of stand selection and subsequent tree selection within the stand (see Figure 5 below). Previous research has demonstrated that these two processes may be partially uncoupled and differentially affected by plant diversity (49, 50).

The effect of resource concentration and frequency on the attraction or repulsion of herbivores in mixed forest stands can be further enhanced by the effects of tree diversity on individual tree apparency. Tree apparency describes how easily insect herbivores can find a tree (135). The apparency of a given tree depends both on its own characteristics (large trees emitting large amounts of host cues are more likely to be found by foraging insect herbivores than smaller, hidden trees) and on those of its neighbors. For instance, a series of studies revealed not only that taller pines (i.e., intrinsically more apparent) were more likely to be attacked by the pine processionary moth
(20, 118), but also that the probability of attack was reduced in the presence of taller nonhost birch trees within and around pine stands (20, 29), and that the protective effect of birch diminished as pines became taller than birches (24). The importance of tree apparency as a mechanism driving tree diversity effects on insect herbivores has been suggested in other model systems, such as the interactions between chestnut (45), oak (20), or birch (97) and their insect herbivores.

### 3.2. Enhanced Regulation of Herbivores by Natural Enemies in Mixed Forests

Very early in the development of the associational resistance theory, several authors postulated that predators and parasitoids are more efficient in controlling herbivore populations in mixed stands than in pure stands (enemies hypothesis) (121, 124). This hypothesis has generated much interest in the field of entomology, and the accumulation of supporting evidence has paved the way for the implementation of biological control methods (131). However, the relevance of the enemies hypothesis in forest ecosystems has been less studied.

The enemies hypothesis is based on two main assumptions. The first is that the abundance or diversity of herbivore natural enemies is positively correlated with plant species richness. Several studies using tree diversity experiments have reported positive correlations between tree species richness and the abundance or diversity of generalist predators such as ants (40, 68, 119, 134), carabids (67), spiders (68, 119), staphylinids (140), and insectivorous birds (101), but others have found neutral effects of tree diversity on ants (15, 140), parasitoid wasps (35), and ground beetles and spiders (10, 106, 107, 127, 130, 140). Surprisingly, few studies found negative effects of tree diversity on the abundance and richness of herbivore natural enemies (129). Similarly, large-scale observational studies in boreal (25) or temperate (4, 96) forests generally report higher abundance or diversity of bats, birds, and spiders in mixed-species forests than in pure forests. However, most authors have pointed out that species composition is more important than species richness in explaining the positive effect of mixing tree species on predator diversity, with a general advantage demonstrated for associating broad-leaf trees with conifers (26, 127, 140).

The second assumption of the enemies hypothesis is that a greater abundance or diversity of herbivore natural enemies in mixed stands is associated with a greater amount of food resources and shelters for herbivore enemies. Because the diversity of insect herbivores generally increases with tree species diversity (21, 46, 103), predatory arthropods or insectivorous bats and birds are more likely to find complementary or supplementary food items and thus maintain higher densities in species-rich forests than in forest monocultures. Adult parasitoids may also benefit from complementary food resources such as pollen, nectar, or honeydew to increase their longevity and fitness (33, 132). As the quantity or diversity of tree microhabitats increases with the number of tree species, natural enemies may find more suitable overwintering, nesting, or resting sites in mixed forests (5). The structural complexity of mixed forests (e.g., higher vertical stratification) would also reduce the risk of intraguild predation by providing more refuges (39).

Nevertheless, enemy-mediated associational resistance in mixed forests cannot be demonstrated solely based on increased abundance or diversity of herbivore enemies with greater tree diversity; mixing tree species should also improve the efficiency of predation or parasitism to achieve associational resistance to insect herbivores. Some correlative studies have reported that the abundance or damage of forest pests decreased with higher densities of predators [e.g., ants (68), bugs (64), or generalist parasitoids (115, 132)] in more diverse forests. However, several experiments exposing live or artificial prey to assess more directly predation or parasitism activity have reported contrasting effects of tree diversity on herbivore parasitism, with higher (16, 86), neutral (119), or lower (55, 86) parasitism rates in mixed forests. In contrast, insectivorous birds have shown a consistent trend toward higher predation rates in more diverse forests (97, 111).
The enhancement of top-down control of herbivores by natural enemies in mixed-species forests is based on two conditions. The first is the ability of local species of predators or parasitoids to switch to different host or prey species, to benefit from different sources of food resources but also to develop specifically at the expense of the target pest species. This condition might explain why the enemies hypothesis has received more consistent support from studies on generalist parasitoids and predators (e.g., birds). The second condition is that a mixture of tree species improves and does not prevent the finding of host trees or herbivores. Insect predators and parasitoids generally use a combination of chemical cues released by insect herbivores (i.e., kairomones) (142) and damaged plants (e.g., jasmonic acid or salicylic acid derivatives involved in indirect predation) (137) to locate their host tree or prey. These processes might be weakened by the lower density of target pests (in the case of associational resistance), disrupted by the release of nonhost volatiles (149), or diverted by more apparent alternative prey in mixed forests. This may explain the inconsistent patterns of pest control by insectivorous arthropods in more diverse forests.

4. EMERGING MECHANISMS AND FUTURE DIRECTIONS

4.1. Indirect Trait-Mediated Effects of Tree Diversity on Insect Herbivory

Researchers have recently recognized that tree diversity can modify tree suitability as a food resource through changes in the nutritional quality or defenses of tree tissues (via changes in physical traits or secondary metabolites), which indirectly affects herbivory (19, 22, 91, 96, 122). In particular, greater tree species diversity is expected to increase tree growth and forest productivity (62, 150). In turn, greater tree vigor should lead to decreased allocation to defenses (and in turn higher herbivory) in diverse systems if these functions trade off (27, 54). Despite growing interest on this topic, results have been inconclusive, with studies showing higher levels of chemical defenses in mixed stands (91), higher levels of physical defenses in pure stands (22), or no effects of tree diversity on tree defenses (19, 96, 122). These contrasting findings show the need for further studies including tree traits related to induced defense (70), tolerance (e.g., regrowth capacity or overcompensation in reproduction) (18), nutritional quality (e.g., nitrogen) (89), or indirect defense promoting herbivore enemy attraction (e.g., volatiles, extrafloral nectar) (76) to provide a better understanding of the mechanisms underlying indirect effects (via tree defenses) of tree species diversity on forest insect pests.

4.2. Intraspecific Diversity Effects

The premise of associational resistance theory is that there are species-specific traits that determine tree–herbivore interactions. Over the past decade, ecologists have started to address the effects of plant intraspecific diversity (i.e., the number of genotypes of a given species in a population) on associated communities of consumers (28, 57), demonstrating, in some cases, that intraspecific genetic diversity in functional traits such as plant growth or defenses was large enough to drive associational resistance effects (2, 58). Results from this research are summarized in a recent meta-analysis of 60 experimental studies reporting that plant genotypic diversity reduces damage by generalist (but not specialist) herbivores, and that this effect was stronger for crops than for wild species, including trees (82). To date, few studies have measured the relative importance or concurrent effects of plant intra- and interspecific diversity on consumers (8, 92). It is hypothesized that species diversity effects on consumers should be stronger than genotypic diversity effects, as the magnitude of plant trait (e.g., growth, defenses, VOCs) variation underlying diversity effects is frequently greater among plant species than among genotypes within a given
**Figure 3**

Herbivore diet breadth and (phylo)genetic distance between a focal tree and its neighbors interactively determine the strength and direction of associational effects in mixed forests. **(Bottom)** The focal tree is represented at the left-hand side of the figure (e.g., an oak). The dendrogram represents the (phylo)genetic distances between tree genotypes (a to c) or species (d, congeneric species; e–g, heterogeneric species), represented by their leaves. The phylogenetic distance between the focal species (a–c) and any associated species (d–g) increases toward the right. **(Top)** Generalist herbivore species (blue lines) can exploit various host tree species and benefit from tree diversity, resulting in associational susceptibility. However, when phylogenetic distance between the focal tree and its neighbors becomes large enough to reduce their suitability as alternative host trees, this could lead to associational resistance (dotted downward curve). Whether mixtures of closely related species or genotypes are detrimental or beneficial to specialist herbivores (red lines) remains unclear (dotted upward curve). However, as soon as the phylogenetic distance between the focal tree and its neighbor expands beyond the genus barrier, associational resistance to specialist herbivores becomes more likely.

species (41). However, the available studies have demonstrated that genotypic diversity effects can be stronger than previously thought (1, 91) for forest diversity experiments. Further studies addressing the relative strength and combined effects of tree intra- and interspecific diversity on the functional contrast between host and nonhost trees are needed to disentangle the ultimate drivers of associational resistance against forest insect pests. In particular, it would be interesting to confirm that the effects of intraspecific diversity are likely to be neutral for generalist herbivores but could be negative (e.g., leading to associative resistance) for monophagous herbivores if genetic differences lead to contrasts in traits relevant to herbivory resistance (Figure 3).

### 4.3. Communication Among Trees

Plants perceive and respond to complex blends of VOCs emitted by conspecific and heterospecific neighboring plants (53, 74). Such responses frequently involve either priming or defense induction by receiver plants when exposed to VOCs released by herbivore-damaged neighbors (emitters), which ultimately results in heightened resistance on the part of the receiver against subsequent herbivory (71). Recent advances in plant chemical communication involving insect herbivory underscore the high degree of specificity in the volatile blends and individual compounds emitted by attacked plants, as well as the specificity in responses to these emissions (90). Studies have
shown that the presence and magnitude of plant responses to VOCs emitted by damaged neighbors are usually (phylo)genetically constrained. For example, plant-to-plant communication may be stronger among related plants than among unrelated plants, presumably dictated by genetically based differentiation in VOC-mediated dialects (72, 73, 95). Therefore, although empirical evidence is still scarce in forests, VOC-mediated communication may be one of the potential mechanisms underlying tree diversity effects on insect herbivory (78). In particular, as VOC-mediated communication has been found to be stronger between emitter and receiver trees from the same genotype or species (90), resistance mediated by communication between neighboring trees might be higher in pure forests than in mixed forests (i.e., associational susceptibility).

### 4.4. Herbivory Pressure

The magnitude and direction of tree species diversity effects on herbivory might be dependent on herbivory pressure. According to the optimal foraging theory (146), natural enemies would also spend less time in forest stands where prey resources are less abundant, making it more difficult to observe associational resistance. If low herbivore population densities are associated with low levels of damage in attacked trees, then this would reduce the likelihood of release of the VOCs that alter the chemical apperancy of host trees, induce a defense reaction in host trees, or increase attraction of natural enemies. Consequently, tree diversity effects on insect herbivory might be more likely to occur at higher herbivory levels. The data collected for our meta-analysis seem to confirm this prediction, as most insect specialist responses to tree diversity were more negative (i.e., greater associational resistance) under high herbivory pressure (Figure 4), while responses of both generalist and specialist herbivores were mostly neutral under low herbivory pressure.

### 4.5. Multitrophic Interactions

The magnitude and direction of tree species diversity effects on herbivory might also be dependent on complex biotic interactions between trees and microbial organisms such as fungi, bacteria, and

![Figure 4](image_url)

Effects of herbivory level on herbivore responses to tree diversity for herbivore specialists and generalists. For each study case of our database, we characterized herbivory pressure as low (blue dots) when the percentage of damage (% defoliation, % attacked trees, or % attacked leaves) was lower than 5% and high (red dots) when the percentage of damage was higher than 5%. Dots represent individual study cases. Their size is proportional to their weight (inverse of variance) in the meta-analysis. White large dots represent the mean effect size, and bars represent standard errors (based on raw data).
viruses. These microbial organisms can modify directly (via herbivore performance or behavior) (36) or indirectly (by modifying host tree quality or natural enemy attraction) (52, 136) tree–insect interactions. Symbiosis between trees and microbes (e.g., mycorrhizae) could also modify tree physiology and tree–insect interactions (80). For example, recent studies using tree diversity experiments have revealed that leaf (84) and soil (32, 77, 120) bacterial diversity and activity increase with increasing tree species richness or functional diversity. Similar tree diversity effects have been observed with mycorrhizae and soil-borne saprophytic fungi (102, 120). In contrast, the incidence of root rot fungi (59) and leaf fungal pathogens (37, 51, 102) has been found to decrease with increasing tree species diversity. The physiological consequences of multiple tree–microbial organism interactions (e.g., through cross talk between signaling pathways in tree defenses against pathogens and herbivores) (137) and the ecological consequences of multitrophic interactions (e.g., through competition, antagonism, or mutualism) (94, 133) should be taken into account to better predict and understand tree diversity effects on insect herbivores. Further work should include a more holistic view of the trophic interactions involved in associational resistance processes in mixed forests, similar to what has been undertaken in grassland experiments (34, 126).

4.6. Bioclimatic Effects

Many studies have pointed out that biodiversity–ecosystem functioning relationships are often dependent on environmental context, with macroclimate conditions (e.g., at regional or continental scales) changing the magnitude and direction of tree diversity effects on ecosystem functioning (117). Large biogeographical analyses along latitudinal or altitudinal gradients have usually reported an increase in herbivore damage at lower latitudes and elevations, which is probably due to positive effects of temperature and precipitation on insect survival and developmental rate (direct effects) (83, 93, 145) and also to reduced levels of plant defenses such as leaf phenolics (indirect effects) (93). However, it has been shown that the positive effects of forest diversity on tree growth (i.e., overyielding) also increase with precipitation (62), leading to a potential decrease of tree defenses in mixed forests at lower latitudes as a result of the growth–differentiation trade-off (54). The increased abundance of insect herbivores at lower latitudes and elevation might be also offset by the greater rate of predation (123) and parasitism (110) in the same regions. However, how these opposing forces might interfere with tree diversity effects to drive associational effects remains unclear. In our meta-analysis, we evaluated how mean annual temperature or precipitation affect the magnitude of associational resistance in mixed forests and found that climatic conditions did not influence herbivory patterns in mixed versus pure forests (Supplemental Appendix).

Local microclimate conditions may also interact with forest composition to influence insect herbivory. For example, in a tree diversity experiment in southwestern France, birch trees growing with heterospecific neighbors had greater levels of leaf chopper damage (i.e., associational susceptibility) and lower concentrations of leaf phenolics, but only under drought (versus irrigated) conditions (22). In contrast, in the same experimental site, pine trees growing in mixtures had lower rates of attacks by the stem borer Dioryctria sylvestrella (i.e., associational resistance) but only under wet conditions (65). These results suggest that insect–tree relationships in mixed forests need to be analyzed taking into account climatic (and other abiotic) conditions at local and large biogeographical scales.

4.7. Exotic Insect Herbivores

Due to the exponential increase in the risks posed by alien insects to forest health, researchers have started questioning the role of tree diversity in resisting these biological invasions. The success
of non-native insect herbivores in the introduced range can be explained by the lack of coevolution, resulting in lower resistance of naïve host trees (i.e., the biotic resistance hypothesis) (13, 109). Novel host trees could be more difficult to detect and colonize by non-native herbivores in mixed-species forest stands, strengthening the effects of host concentration and host apparency. For instance, studies have found that chestnut resistance to the invasive Asian gall wasp increased with an increasing proportion of nonhost neighboring trees (35, 44).

Non-native pests might also be more damaging due to the lack of effective top-down control by their natural enemies (i.e., the enemy release hypothesis) (88). However, according to the natural enemy hypothesis, increasing tree diversity might enhance top-down control of exotic insect herbivores by generalist predators (i.e., associational resistance) because diverse systems provide more resources and refuges for those herbivores’ natural enemies. Jactel et al. (64) found that native predatory bugs were more abundant in diverse forests and consequently reduced the incidence of the invasive pine bast scale *Matsucoccus feytaudi* in these forests. The composition of the community of native parasitoids in galls made by the invasive Asian wasp on chestnuts was also different in mixed stands and in pure stands (35), although there was no clear evidence of the resulting effects on the top-down control of the invasive pest. The paucity of studies on the topic calls for more research investigating whether mixed-species forests are more (or less) resistant to non-native pests than are pure forests and to better understand the mechanisms underlying such associational effects.

5. CONCLUSIONS

Based on the results of our meta-analysis and the reexamination of the possible effects of tree diversity on forest resistance to insect pests, and in line with the landing theory developed by Finch & Collier (38), we propose an updated and chronological view of how herbivore diet breadth underlies associational resistance in mixed forests (Figure 5).

5.1. Case of Specialist Herbivores

The first step in the associational resistance process is colonization by insect herbivores of the host tree in mixed stands. During this phase, specialist insect herbivores use long-distance olfactory cues (e.g., VOCs) to recognize a favorable host, e.g., either deciduous or coniferous trees, while selectively avoiding nonhosts. At shorter distances, specialist insect herbivores continue to use olfactory cues (probably more species-specific host recognition signals), but also visual signals linked to tree shape, color, or foliage. Because the number and frequency of host trees are lower in the mixed stand, the probability of host tree detection and encounter by specialist insect herbivores is lower. In addition, the presence of nonhost trees reduces the apparency of these host trees and creates a diversion. During this exploratory phase, specialist insect herbivores may spend more time searching for their host, becoming more exposed to their natural enemies, especially mobile generalist predators such as birds or bats that are able to spot adult insects. Once the insects reach their host tree, they probe the quality of the food (gustation) for their own needs or to ensure better survival of their offspring. Quality or toxicity traits (e.g., chemical defenses) of trees can be modified by the neighborhood effect of heterospecific trees via modifications of the abiotic environment (microclimate, shading) or the emission of alert signals (communication between trees, above or below ground). A reduction of tree nutritional quality can then lead to tree rejection by the ovipositing female or a deleterious effect on the offspring (larvae) if females finally choose to lay eggs. The larval stages developing on the host tree are in turn exposed to predation and parasitism, which are more intense in mixed forests due to the greater stability of natural enemy populations favored by the diversity of food resources and resting or breeding sites.
Conceptual diagram showing how neighborhood diversity around a focal tree (in this case, a conifer species surrounded by two deciduous tree species) can reduce the damage caused by a specialist forest insect (in this case, a moth caterpillar) through bottom-up (mediated by nonhost trees) and top-down (mediated by natural enemies, in this case, birds, parasitoids, and spiders) forces at the successive stages of host tree recognition (search and find), colonization (choose), and exploitation (consume).

### 5.2. Case of Generalist Herbivores

During the first stage of forest stand colonization, generalist insect herbivores can be favored by a greater diversity of tree species in a mixed forest because they have a wider array of potential hosts given their large diet breadth. The effects of reducing the probability of host encountering due to lower frequency or apparency are no longer effective. Similarly, the reduction in food quality induced by the presence of heterospecific neighbors has less effect on the choice of host tree by the adult generalist or on the survival of its progeny due to the greater tolerance of these organisms. Conversely, generalist insect herbivores may benefit from a greater diversity of tree species in a mixed forest because of the beneficial effect of a mixed diet. However, generalist insect herbivores remain exposed to greater predation or parasitism pressure. Finally, positive effects of species mixtures on generalist herbivores decrease as the functional (or phylogenetic) diversity of the mixed species increases. Diversity effects might become as negative as they are for specialist herbivores if the associated tree species are highly contrasted in terms of host quality, going beyond the limits of their diet.

### 5.3. Management Implications

The observation that associational resistance intensity in mixed forests increases when pest population levels are greater would imply that increasing forest diversity is a promising management
tool to reduce pest damage. We provide some forest management recommendations based on the mechanistic model outlined above. In terms of choosing the composition of mixed forests, the association of tree species with highly contrasting functional characteristics (e.g., deciduous and coniferous species) should be favored. However, these differences in tree traits should mainly affect the processes involved in host recognition (e.g., host versus nonhost volatiles) and resources for natural enemies (e.g., alternative food or shelters). The choice of a companion species according to the criteria of growth and productivity is more difficult. An associated species with a growth rate that is too low compared to that of the species to be protected would not reduce its apparency, nor would it promote diversion. Forest owners might be reluctant to grow species with low productivity in terms of wood products. Species with very contrasting growth rates will pose silvicultural management issues, with different thinning regimes and harvesting ages. The spatial arrangement of different species within the mixed forest is also important. It is undeniable that a tree-to-tree species mixing pattern is the most efficient, as it would lead to a more difficult search for a host tree and increase neighborhood effects on trait modification. However, this type of mixing is more difficult to manage in mechanized production forests such as tree plantations. An interesting alternative would be to design and test mixed plantations in alternating strips (row-wise pattern; 30) because it would allow for differentiated silviculture while maintaining close proximity between different species. Finally, one solution with lower impact on forest managers (particularly in the case of intensively managed plantations) is the establishment of mixed hedges surrounding a pure stand of the focal species. Mixed-species hedges can limit host tree accessibility for insect herbivores and serve as a habitat for natural enemies. Ultimately, the choice among these forest diversification options must be based on a multidisciplinary analysis of the technical, economical, and societal constraints.

DISCLOSURE STATEMENT

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LITERATURE CITED


86. Legault S, James PMA. 2018. Parasitism rates of spruce budworm larvae: testing the enemy hypothesis along a gradient of forest diversity measured at different spatial scales. *Environ. Entomol.* 47:1083–95


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