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

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## Keywords

biodiversity, herbivory, associational resistance, host concentration, defense traits, natural enemies

## 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 herbivor* 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 WorldClim 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 ($I^2$, $\tau^2$, and 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
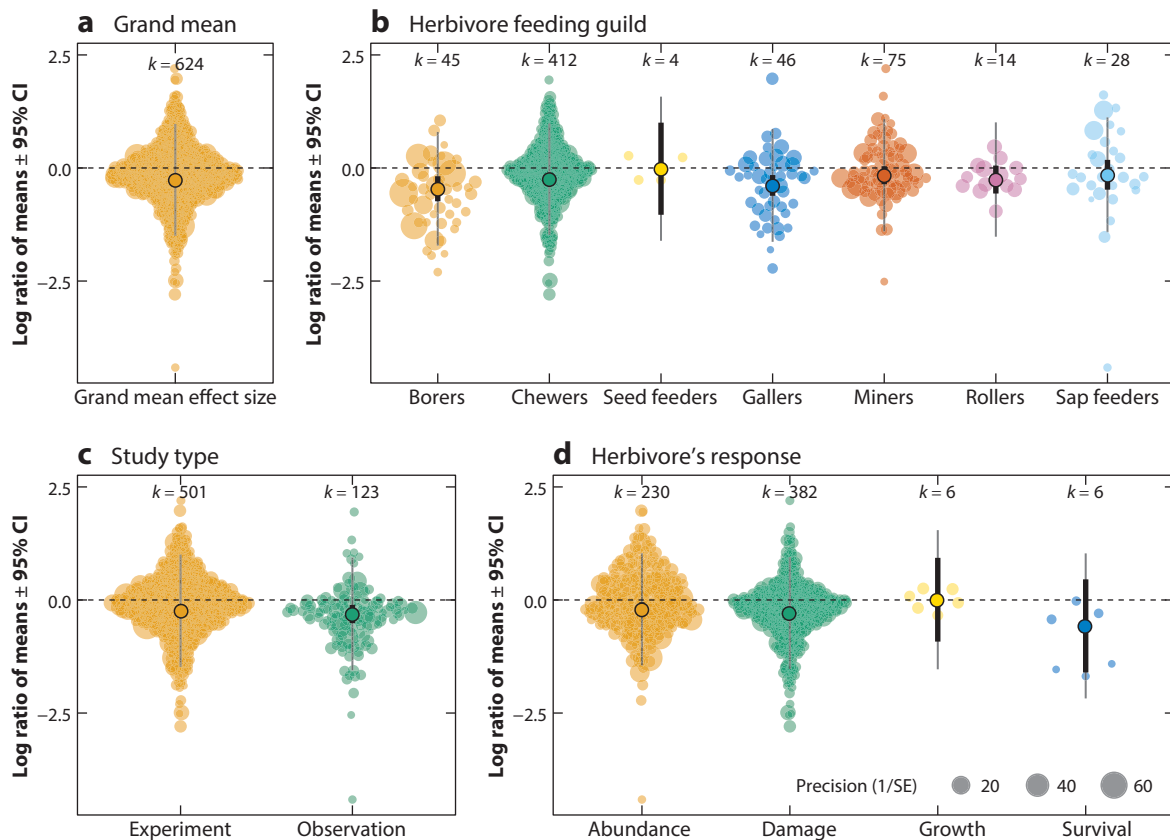
**Figure 1**

Summary of tree diversity effects on insect herbivores. (*a*) Grand mean effect size. (*b*) Grand mean effect size calculated for each herbivore feeding guild. (*c*) Grand mean effect size for experimental versus observational studies. (*d*) Grand mean effect size calculated for each type of herbivore response. Dots represent individual study cases. Dot size is proportional to the precision of each study case [i.e., the reciprocal of its standard error (SE)]. Black circled dots represent the mean effect size for each moderator level. Vertical thick lines represent the 95% confidence interval (CI) (they may be hidden by circles representing the mean effect sizes when they are very low). Thin vertical lines represent the prediction interval, which is the expected range of true effects in similar studies. *k* indicates the number of study cases for each moderator level.

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% 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 1*a***). This result was consistent across herbivore feeding guilds (**Figure 1*b***), study types (**Figure 1*c***), and types of herbivore responses (**Figure 1*d***). 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
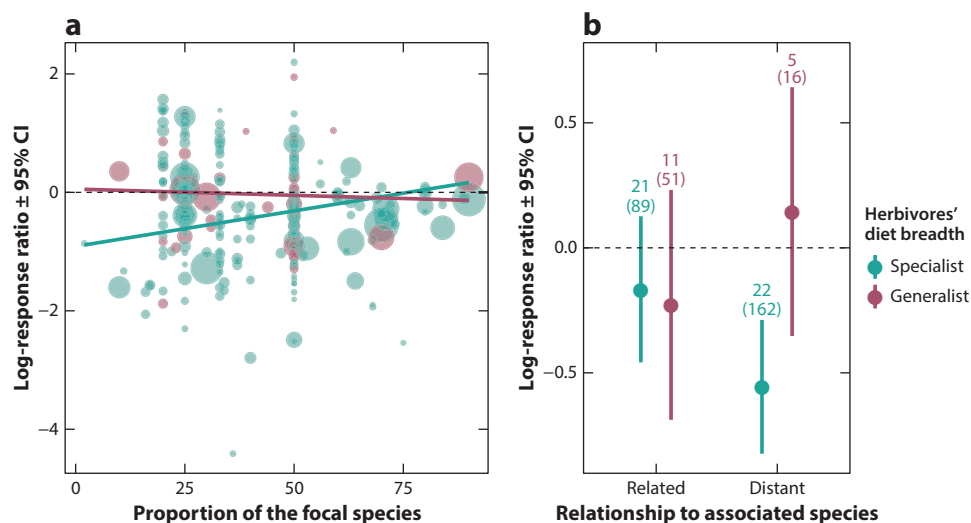


**Figure 2**

Effects of focal host frequency in mixed stands, composition of mixed stands (with phylogenetically distant or related species, i.e., gymnosperms and angiosperms), and herbivore diet breadth on the response of insect herbivores to tree species diversity. (*a*) Dots represent individual study cases. Their size is proportional to their weight (inverse of variance) in the meta-analysis. Regression lines represent the averaged predictions of the two models with ΔAICc < 2. (*b*) Dots represent mean effect size, and bars represent confidence intervals (based on model predictions averaged across the two models with ΔAICc < 2). Numbers indicate the number of primary studies (articles) and study cases (within parentheses). Abbreviations: AICc, Akaike's Information Criterion corrected for small sample size; CI, confidence interval.

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 chewers (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
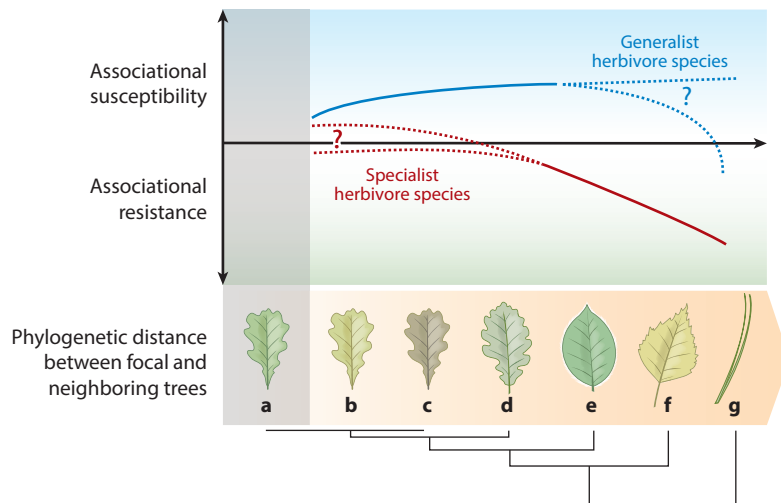
**Figure 3**

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 herbivore species (*red lines*) remains unclear (*dotted upward curves*). 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 apparency 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
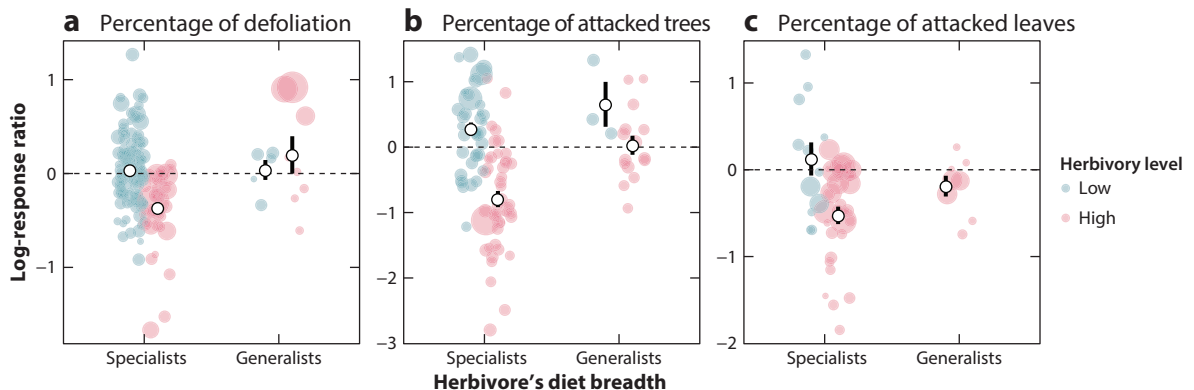
**Figure 4**

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 chewer 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.
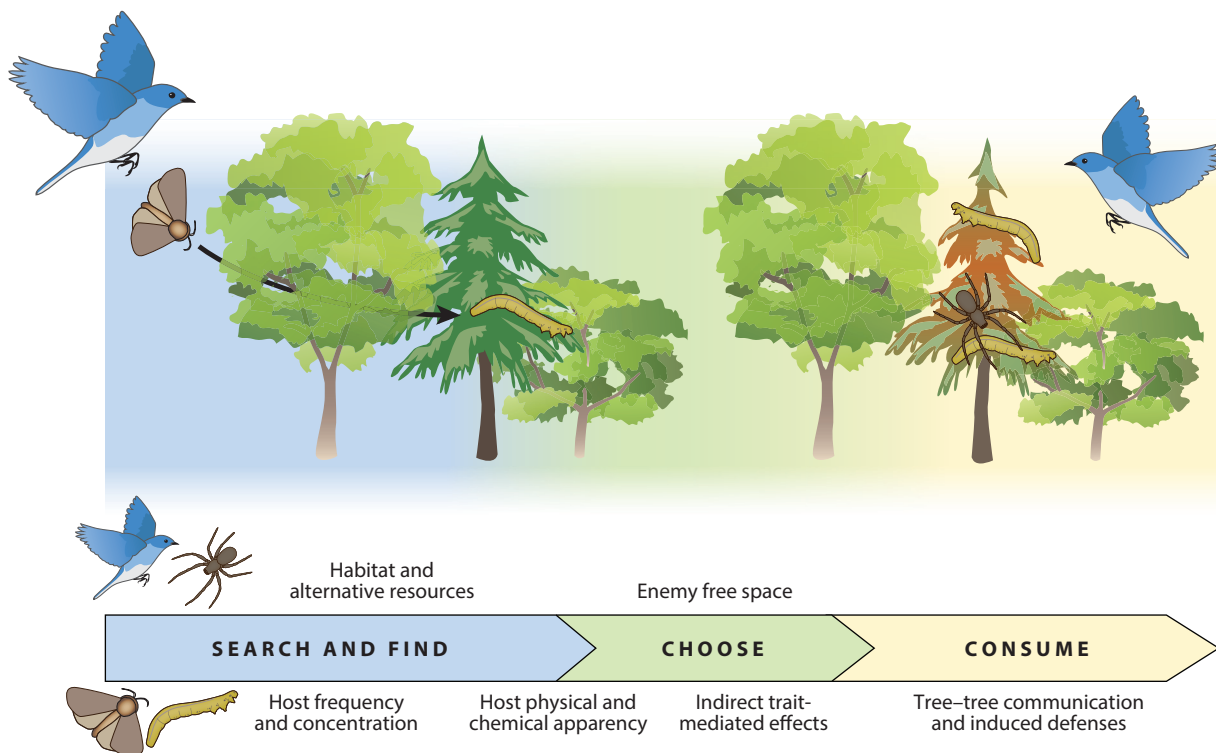
**Figure 5**

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 hedgerows 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

## ACKNOWLEDGMENTS

## LITERATURE CITED

1. Abdala-Roberts L, Mooney KA, Quijano-Medina T, Campos-Navarrete MJ, González-Moreno A, Parra-Tabla V. 2015. Comparison of tree genotypic diversity and species diversity effects on different guilds of insect herbivores. *Oikos* 124:1527–35
2. Abdala-Roberts L, Pratt J, Pratt R, Schreck T, Hannah V, Mooney KA. 2016. Multi-trophic consequences of plant genetic variation in sex and growth. *Ecology* 97:743–53
3. Abdala-Roberts L, Puentes A, Finke DL, Marquis RJ, Montserrat-Larrosa M, et al. 2019. Tri-trophic interactions: bridging species, communities, and ecosystems. *Ecol. Lett.* 22:2151–67
4. Ampoorter E, Barbaro L, Jactel H, Baeten L, Boberg J, et al. 2020. Tree diversity is key for promoting the diversity and abundance of forest-associated taxa in Europe. *Oikos* 129:133–46
5. Asbeck T, Pyttel P, Frey J, Bauhus J. 2018. Predicting abundance and diversity of tree-related microhabitats in Central European montane forests from common forest attributes. *Forest Ecol. Manag.* 432:400–8

6.  Atsatt PR, O'Dowd DJ. 1976. Plant defense guilds. *Science* 193:24–29

7.  Bañuelos M-J, Kollmann J. 2011. Effects of host-plant population size and plant sex on a specialist leaf-miner. *Acta Oecol.* 37:58–64

8.  Barantal S, Castagneyrol B, Durka W, Iason G, Morath S, Koricheva J. 2019. Contrasting effects of tree species and genetic diversity on the leaf-miner communities associated with silver birch. *Oecologia* 189:687–97

9.  Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szendrei Z. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. *Annu. Rev. Ecol. Evol. Syst.* 40:1–20

10. Barsoum N, Fuller L, Ashwood F, Reed K, Bonnet-Lebrun A-S, Leung F. 2014. Ground-dwelling spider (Araneae) and carabid beetle (Coleoptera: Carabidae) community assemblages in mixed and monoculture stands of oak (*Quercus robur* L./*Quercus petraea* (Matt.) Liebl.) and Scots pine (*Pinus sylvestris* L.). *Forest Ecol. Manag.* 321:29–41

11. Bognounou F, De Grandpré L, Pureswaran DS, Kneeshaw D. 2017. Temporal variation in plant neighborhood effects on the defoliation of primary and secondary hosts by an insect pest. *Ecosphere* 8:e01759

12. Brezzi M, Schmid B, Niklaus PA, Schuldt A. 2017. Tree diversity increases levels of herbivore damage in a subtropical forest canopy: evidence for dietary mixing by arthropods? *J. Plant Ecol.* 10:13–27

13. Brockerhoff EG, Liebhold AM. 2017. Ecology of forest insect invasions. *Biol. Invasions* 19:3141–59

14. Campbell SA, Borden JH. 2009. Additive and synergistic integration of multimodal cues of both hosts and non-hosts during host selection by woodboring insects. *Oikos* 118:553–63

15. Campos-Navarrete MJ, Abdala-Roberts L, Munguía-Rosas M, Parra-Tabla V. 2015. Are tree species diversity and genotypic diversity effects on insect herbivores mediated by ants? *PLOS ONE* 10:e0132671

16. Cappuccino N, Lavertu D, Bergeron Y, Régnière J. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia* 114:236–42

17. Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, et al. 2012. Biodiversity loss and its impact on humanity. *Nature* 486:59–67

18. Carmona D, Lajeunesse MJ, Johnson MTJ. 2011. Plant traits that predict resistance to herbivores. *Funct. Ecol.* 25:358–67

19. Castagneyrol B, Bonal D, Damien M, Jactel H, Meredieu C, et al. 2017. Bottom-up and top-down effects of tree species diversity on leaf insect herbivory. *Ecol. Evol.* 7:3520–31

20. Castagneyrol B, Giffard B, Pére C, Jactel H. 2013. Plant apparency, an overlooked driver of associational resistance to insect herbivory. *J. Ecol.* 101:418–29

21. Castagneyrol B, Jactel H. 2012. Unraveling plant-animal diversity relationships: a meta-regression analysis. *Ecology* 93:2115–24

22. Castagneyrol B, Jactel H, Moreira X. 2018. Anti-herbivore defences and insect herbivory: interactive effects of drought and neighbours. *J. Ecol.* 106:2043–57

23. Castagneyrol B, Jactel H, Vacher C, Brockerhoff EG, Koricheva J. 2014. Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. *J. Appl. Ecol.* 51:134–41

24. Castagneyrol B, Kozlov MV, Poeydebat C, Toïgo M, Jactel H. 2020. Associational resistance to a pest insect fades with time. *J. Pest Sci.* 93:427–37

25. Cavard X, Macdonald SE, Bergeron Y, Chen HYH. 2011. Importance of mixedwoods for biodiversity conservation: evidence for understory plants, songbirds, soil fauna, and ectomycorrhizae in northern forests. *Environ. Rev.* 19:142–61

26. Charbonnier YM, Barbaro L, Barnagaud JY, Ampoorter E, Nezan J, et al. 2016. Bat and bird diversity along independent gradients of latitude and tree composition in European forests. *Oecologia* 182:529–37

27. Coley PD, Bryant JP, Chapin FS. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895–99

28. Crutsinger GM, Collins MD, Fordyce JA, Gompert Z, Nice CC, Sanders NJ. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* 313:966–68

29. Damien M, Jactel H, Meredieu C, Régolini M, Van Halder I, Castagneyrol B. 2016. Pest damage in mixed forests: disentangling the effects of neighbor identity, host density and host apparency at different spatial scales. *Forest Ecol. Manag.* 378:103–10

30. del Río M, Pretzsch H, Alberdi I, Bielak K, Bravo F, et al. 2018. Characterization of mixed forests. In *Dynamics, Silviculture and Management of Mixed Forests*, ed. A Bravo-Oviedo, H Pretzsch, M del Río, pp. 27–71. Berlin: Springer

31. Dinnage R. 2013. Phylogenetic diversity of plants alters the effect of species richness on invertebrate herbivory. *PeerJ.* 1:e93

32. Dukunde A, Schneider D, Schmidt M, Veldkamp E, Daniel R. 2019. Tree species shape soil bacterial community structure and function in temperate deciduous forests. *Front. Microbiol.* 10:1519

33. Dulaurent AM, Porté AJ, Van Halder I, Vétillard F, Menassieu P, Jactel H. 2012. Hide and seek in forests: Colonization by the pine processionary moth is impeded by the presence of nonhost trees. *Agric. For. Entomol.* 14:19–27

34. Eisenhauer N, Bonkowski M, Brose U, Buscot F, Durka W, et al. 2019. Biotic interactions, community assembly, and eco-evolutionary dynamics as drivers of long-term biodiversity-ecosystem functioning relationships. *Res. Ideas Outcomes* 5:e47042

35. Fernández-Conradi P, Borowiec N, Capdevielle X, Castagneyrol B, Maltoni A, et al. 2018. Plant neighbour identity and invasive pathogen infection affect associational resistance to an invasive gall wasp. *Biol. Invasions* 20:1459–73

36. Fernández-Conradi P, Jactel H, Robin C, Tack AJM, Castagneyrol B. 2018. Fungi reduce preference and performance of insect herbivores on infected plants. *Ecology* 99:300–11

37. Field E, Schönrogge K, Barsoum N, Hector A, Gibbs M. 2019. Individual tree traits shape insect and disease damage on oak in a climate-matching tree diversity experiment. *Ecol. Evol.* 9:8524–40

38. Finch S, Collier R. 2000. Host-plant selection by insects: a theory based on "appropriate/inappropriate landings" by pest insects of cruciferous plants. *Entomol. Exp. Appl.* 96:91–102

39. Finke DL, Denno RF. 2004. Predator diversity dampens trophic cascades. *Nature* 429:407–10

40. Fornoff F, Klein AM, Blüthgen N, Staab M. 2019. Tree diversity increases robustness of multi-trophic interactions. *Proc. R. Soc. B* 286:20182399

41. Fridley JD, Grime PJ. 2010. Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology* 91:2272–83

42. Griscom BW, Adams J, Ellis PW, Houghton RA, Lomax G, et al. 2017. Natural climate solutions. *PNAS* 114:11645–50

43. Grossman JJ, Vanhellemont M, Barsoum N, Bauhus J, Bruelheide H, et al. 2018. Synthesis and future research directions linking tree diversity to growth, survival, and damage in a global network of tree diversity experiments. *Environ. Exp. Bot.* 152:68–69

44. Guyot V, Castagneyrol B, Vialatte A, Deconchat M, Jactel H. 2016. Tree diversity reduces pest damage in mature forests across Europe. *Biol. Lett.* 12:20151037

45. Guyot V, Castagneyrol B, Vialatte A, Deconchat M, Selvi F, et al. 2015. Tree diversity limits the impact of an invasive forest pest. *PLOS ONE* 10:e0136469

46. Guyot V, Jactel H, Imbaud B, Burnel L, Castagneyrol B, et al. 2019. Tree diversity drives associational resistance to herbivory at both forest edge and interior. *Ecol. Evol.* 9:9040–51

47. Haase J, Castagneyrol B, Cornelissen JHC, Ghazoul J, Kattge J, et al. 2015. Contrasting effects of tree diversity on young tree growth and resistance to insect herbivores across three biodiversity experiments. *Oikos* 124:1674–85

48. Hahn PG, Orrock JL. 2016. Neighbor palatability generates associational effects by altering herbivore foraging behavior. *Ecology* 97:2103–11

49. Hambäck PA, Björkman M, Hopkins RJ. 2010. Patch size effects are more important than genetic diversity for plant-herbivore interactions in *Brassica* crops. *Ecol. Entomol.* 35:299–306

50. Hambäck PA, Inouye BD, Andersson P, Underwood N. 2014. Effects of plant neighborhoods on plant-herbivore interactions: resource dilution and associational effects. *Ecology* 95:1370–83

51. Hantsch L, Braun U, Scherer-Lorenzen M, Bruelheide H. 2013. Species richness and species identity effects on occurrence of foliar fungal pathogens in a tree diversity experiment. *Ecosphere* 4:1–12

52. Hare JD. 2011. Ecological role of volatiles produced by plants in response to damage by herbivorous insects. *Annu. Rev. Entomol.* 56:161–80

53. Heil M, Karban R. 2010. Explaining the evolution of plant communication by airborne signals. *Trends Ecol. Evol.* 25:137–44

54. Herms DA, Mattson WJ. 1992. The dilemma of plants: to grow or defend. *Q. Rev. Biol.* 67:283–335

55. Herz A, Heitland W. 2005. Species diversity and niche separation of cocoon parasitoids in different forest types with endemic populations of their host, the common pine sawfly *Diprion pini* (Hymenoptera: Diprionidae). *Eur. J. Entomol.* 102:217–24

56. Holmes SB, MacQuarrie CJ. 2016. Chemical control in forest pest management. *Can. Entomol.* 148:S270–95

57. Hughes AR. 2014. Genotypic diversity and trait variance interact to affect marsh plant performance. *J. Ecol.* 102:651–58

58. Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M. 2008. Ecological consequences of genetic diversity. *Ecol. Lett.* 11:609–23

59. Jactel H, Bauhus J, Boberg J, Bonal D, Castagneyrol B, et al. 2017. Tree diversity drives forest stand resistance to natural disturbances. *Curr. For. Rep.* 3:223–43

60. Jactel H, Birgersson G, Andersson S, Schlyter F. 2011. Non-host volatiles mediate associational resistance to the pine processionary moth. *Oecologia* 166:703–11

61. Jactel H, Brockerhoff EG. 2007. Tree diversity reduces herbivory by forest insects. *Ecol. Lett.* 10:835–48

62. Jactel H, Gritti ES, Drössler L, Forrester DI, Mason WL, et al. 2018. Positive biodiversity-productivity relationships in forests: Climate matters. *Biol. Lett.* 14:20170747

63. Jactel H, Koricheva J, Castagneyrol B. 2019. Responses of forest insect pests to climate change: not so simple. *Curr. Opin. Insect Sci.* 35:103–8

64. Jactel H, Menassieu P, Vetillard F, Gaulier A, Samalens JC, Brockerhoff EG. 2006. Tree species diversity reduces the invasibility of maritime pine stands by the bast scale, *Matsucoccus feytaudi* (Homoptera: Margarodidae). *Can. J. For. Res.* 36:314–23

65. Jactel H, Poeydebat C, van Halder I, Castagneyrol B. 2019. Interactive effects of tree mixing and drought on a primary forest pest. *Front. For. Glob. Change* 2:77

66. Jactel H, Verheggen F, Thiéry D, Escobar-Gutiérrez AJ, Gachet E, et al. 2019. Alternatives to neonicotinoids. *Environ. Int.* 129:423–29

67. Jouveau S, Toïgo M, Giffard B, Castagneyrol B, Van Halder I, et al. 2019. Carabid activity-density increases with forest vegetation diversity at different spatial scales. *Insect Conserv. Divers.* 13:36–46

68. Kaitaniemi P, Riihimäki J, Koricheva J, Vehviläinen H. 2007. Experimental evidence for associational resistance against the European pine sawfly in mixed tree stands. *Silva Fenn.* 41:259–68

69. Kambach S, Kühn I, Castagneyrol B, Bruelheide H. 2016. The impact of tree diversity on different aspects of insect herbivory along a global temperature gradient: a meta-analysis. *PLOS ONE* 11:e0165815

70. Karban R. 2011. The ecology and evolution of induced resistance against herbivores. *Funct. Ecol.* 25:339–47

71. Karban R. 2015. *Plant Sensing and Communication*. Chicago: Univ. Chicago Press

72. Karban R, Wetzel WC, Shiojiri K, Ishizaki S, Ramirez SR, Blande JD. 2014. Deciphering the language of plant communication: volatile chemotypes of sagebrush. *New Phytol.* 204:380–85

73. Karban R, Wetzel WC, Shiojiri K, Pezzola E, Blande JD. 2016. Geographic dialects in volatile communication between sagebrush individuals. *Ecology* 97:2917–24

74. Karban R, Yang LH, Edwards KF. 2014. Volatile communication between plants that affects herbivory: a meta-analysis. *Ecol. Lett.* 17:44–52

75. Kenis M, Hurley BP, Hajek AE, Cock MJW. 2017. Classical biological control of insect pests of trees: facts and figures. *Biol. Invasions* 19:3401–17

76. Kessler A, Heil M. 2011. The multiple faces of indirect defences and their agents of natural selection. *Funct. Ecol.* 25:348–57

77. Khlifa R, Paquette A, Messier C, Reich PB, Munson AD. 2017. Do temperate tree species diversity and identity influence soil microbial community function and composition? *Ecol. Evol.* 7:7965–74

78. Kigathi RN, Weisser WW, Reichelt M, Gershenzon J, Unsicker SB. 2019. Plant volatile emission depends on the species composition of the neighboring plant community. *BMC Plant Biol.* 19:58

79. Kim TN, Underwood N. 2015. Plant neighborhood effects on herbivory: Damage is both density and frequency dependent. *Ecology* 96:1431–37

80. Koricheva J, Gange AC, Jones T. 2009. Effects of mycorrhizal fungi on insect herbivores: a meta-analysis. *Ecology* 90:2088–97

81. Koricheva J, Gurevitch J, Mengersen K. 2013. *Handbook of Meta-Analysis in Ecology and Evolution*. Princeton, NJ: Princeton Univ. Press

82. Koricheva J, Hayes D. 2018. The relative importance of plant intraspecific diversity in structuring arthropod communities: a meta-analysis. *Funct. Ecol.* 32:1704–17

83. Kozlov MV, Lanta V, Zverev V, Zvereva EL. 2015. Global patterns in background losses of woody plant foliage to insects. *Glob. Ecol. Biogeogr.* 24:1126–35

84. Laforest-Lapointe I, Paquette A, Messier C, Kembel SW. 2017. Leaf bacterial diversity mediates plant diversity and ecosystem function relationships. *Nature* 546:145–47

85. Lefcheck JS, Whalen MA, Davenport TM, Stone JP, Duffy JE. 2013. Physiological effects of diet mixing on consumer fitness: a meta-analysis. *Ecology* 94:565–72

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

87. Letourneau DK, Armbrecht I, Salguero-Rivera B, Montoya-Lerma J, Jiménez-Carmona E, et al. 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecol. Appl.* 21:9–21

88. Liu H, Stiling P. 2006. Testing the enemy release hypothesis: a review and meta-analysis. *Biol. Invasions* 8:1535–45

89. Mattson WJ. 1980. Herbivory in relation to plant nitrogen content. *Annu. Rev. Ecol. Evol. Syst.* 11:119–61

90. Moreira X, Abdala-Roberts L. 2019. Specificity and context-dependency of plant-plant communication in response to insect herbivory. *Curr. Opin. Insect Sci.* 32:15–21

91. Moreira X, Abdala-Roberts L, Parra-Tabla V, Mooney KA. 2014. Positive effects of plant genotypic and species diversity on anti-herbivore defenses in a tropical tree species. *PLOS ONE* 9:e105438

92. Moreira X, Abdala-Roberts L, Rasmann S, Castagneyrol B, Mooney KA. 2016. Plant diversity effects on insect herbivores and their natural enemies: current thinking, recent findings, and future directions. *Curr. Opin. Insect Sci.* 14:1–7

93. Moreira X, Castagneyrol B, Abdala-Roberts L, Berny-Mier y Terán JC, Timmermans BGH, et al. 2018. Latitudinal variation in plant chemical defences drives latitudinal patterns of leaf herbivory. *Ecography* 41:1124–34

94. Moreira X, Mooney KA, Zas R, Sampedro L. 2012. Bottom-up effects of host-plant species diversity and top-down effects of ants interactively increase plant performance. *Proc. R. Soc. B* 279:4464–72

95. Moreira X, Petry WK, Hernández-Cumplido J, Morelon S, Benrey B. 2016. Plant defence responses to volatile alert signals are population-specific. *Oikos* 125:950–56

96. Muiruri EW, Barantal S, Iason GR, Salminen JP, Perez-Fernandez E, Koricheva J. 2019. Forest diversity effects on insect herbivores: Do leaf traits matter? *New Phytol.* 221:2250–60

97. Muiruri EW, Rainio K, Koricheva J. 2016. Do birds see the forest for the trees? Scale-dependent effects of tree diversity on avian predation of artificial larvae. *Oecologia* 180:619–30

98. Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–58

99. Nakadai R, Murakami M, Hirao T. 2014. Effects of phylogeny, leaf traits, and the altitudinal distribution of host plants on herbivore assemblages on congeneric *Acer* species. *Oecologia* 175:1237–45

100. Nakagawa S, Noble DWA, Senior AM, Lagisz M. 2017. Meta-evaluation of meta-analysis: ten appraisal questions for biologists. *BMC Biol.* 15:18

101. Nell CS, Abdala-Roberts L, Parra-Tabla V, Mooney KA. 2018. Tropical tree diversity mediates foraging and predatory effects of insectivorous birds. *Proc. R. Soc. B* 285:20181842

102. Nguyen D, Castagneyrol B, Bruelheide H, Bussotti F, Guyot V, et al. 2016. Fungal disease incidence along tree diversity gradients depends on latitude in European forests. *Ecol. Evol.* 6:2426–38

103. O'Brien MJ, Brezzi M, Schuldt A, Zhang JY, Ma K, et al. 2017. Tree diversity drives diversity of arthropod herbivores, but successional stage mediates detritivores. *Ecol. Evol.* 7:8753–60

104. Ollikainen M. 2014. Forestry in bioeconomy: smart green growth for the humankind. *Scand. J. For. Res.* 29:360–66

105. Otway S, Hector A, Lawton JH. 2005. Resource dilution effects on specialist insect herbivores in a grassland biodiversity experiment. *J. Am. Ecol.* 74:234–40

106. Oxbrough A, French V, Irwin S, Kelly TC, Smiddy P, O'Halloran J. 2012. Can mixed species stands enhance arthropod diversity in plantation forests? *Forest Ecol. Manag.* 270:11–18

107. Oxbrough A, García-Tejero S, Spence J, O'Halloran J. 2016. Can mixed stands of native and non-native tree species enhance diversity of epigaeic arthropods in plantation forests? *Forest Ecol. Manag.* 367:21–29

108. Paquette A, Hector A, Castagneyrol B, Vanhellemont M, Koricheva J, et al. 2018. A million and more trees for science. *Nat. Ecol. Evol.* 2:273–76

109. Pearse IS, Harris DJ, Karban R, Sih A. 2013. Predicting novel herbivore-plant interactions. *Oikos* 122:1554–64

110. Péré C, Jactel H, Kenis M. 2013. Response of insect parasitism to elevation depends on host and parasitoid life-history strategies. *Biol. Lett.* 9:20130028

111. Poch TJ, Simonetti JA. 2013. Ecosystem services in human-dominated landscapes: insectivory in agroforestry systems. *Agrofor. Syst.* 87:871–79

112. Pollastrini M, Nogales AG, Benavides R, Bonal D, Finer L, et al. 2017. Tree diversity affects chlorophyll *a* fluorescence and other leaf traits of tree species in a boreal forest. *Tree Physiol.* 37:199–208

113. Pretzsch H, Forrester DI, Bauhus J. 2017. *Mixed-Species Forests, Ecology and Management*. Berlin: Springer

114. Prokopy RJ, Owens ED. 2003. Visual detection of plants by herbivorous insects. *Annu. Rev. Entomol.* 28:337–64

115. Quayle D, Régnière J, Cappuccino N, Dupont A. 2003. Forest composition, host-population density, and parasitism of spruce budworm *Choristoneura fumiferana* eggs by *Trichogramma minutum*. *Entomol. Exp. Appl.* 107:215–27

116. R Core Team. 2019. R: a language and environment for statistical computing. *Statistical Software*. **http://www.R-project.org/**

117. Ratcliffe S, Wirth C, Jucker T, van der Plas F, Scherer-Lorenzen M, et al. 2017. Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecol. Lett.* 20:1414–26

118. Régolini M, Castagneyrol B, Dulaurent-Mercadal A-M, Piou D, Samalens J-C, Jactel H. 2014. Effect of host tree density and apparency on the probability of attack by the pine processionary moth. *Forest Ecol. Manag.* 334:185–92

119. Riihimäki J, Kaitaniemi P, Koricheva J, Vehviläinen H. 2005. Testing the enemy hypothesis in forest stands: the important role of tree species composition. *Oecologia* 142:90–97

120. Rivest M, Whalen JK, Rivest D. 2019. Tree diversity is not always a strong driver of soil microbialdiversity: a 7-yr-old diversity experiment with trees. *Ecosphere* 10:e02685

121. Root RB. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43:95–124

122. Rosado-Sánchez S, Parra-Tabla V, Betancur-Ancona D, Moreira X, Abdala-Roberts L. 2018. Effects of tree species diversity on insect herbivory and leaf defenses in *Cordia dodecandra*. *Ecol. Entomol.* 43:703–11

123. Roslin T, Hardwick B, Novotny V, Petry WK, Andrew N, et al. 2017. Higher predation risk for insect prey at low latitudes and elevations. *Science* 356:742–44

124. Russell EP. 1989. Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. *Environ. Entomol.* 18:590–99

125. Ruttan A, Lortie CJ. 2015. A systematic review of the attractant-decoy and repellent-plant hypotheses: Do plants with heterospecific neighbours escape herbivory? *J. Plant Ecol.* 8:337–46

126. Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, et al. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468:553–56

127. Schuldt A, Assmann T, Bruelheide H, Durka W, Eichenberg D, et al. 2014. Functional and phylogenetic diversity of woody plants drive herbivory in a highly diverse forest. *New Phytol.* 202:864–73

128. Schuldt A, Baruffol M, Böhnke M, Bruelheide H, Härdtle W, et al. 2010. Tree diversity promotes insect herbivory in subtropical forests of south-east China. *J. Ecol.* 98:917–26

129. Schuldt A, Both S, Bruelheide H, Hardtle W, Schmid B, et al. 2011. Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. *PLOS ONE* 6:e22905

130. Schuldt A, Fahrenholz N, Brauns M, Migge-Kleian S, Platner C, Schaefer M. 2008. Communities of ground-living spiders in deciduous forests: Does tree species diversity matter? *Biodivers. Conserv.* 17:1267–84

131. Shields MW, Johnson AC, Pandey S, Cullen R, González-Chang M, et al. 2019. History, current situation and challenges for conservation biological control. *Biol. Control* 131:25–35

132. Simmons GA, Leonard DE, Chen CW. 1975. Influence of tree species density and composition on parasitism of the spruce budworm, *Choristoneura fumiferana* (Clem.). *Environ. Entomol.* 4:832–36

133. Staab M, Blüthgen N, Klein A-M. 2015. Tree diversity alters the structure of a tri-trophic network in a biodiversity experiment. *Oikos* 124:827–34

134. Staab M, Schuldt A, Assmann T, Klein A-M. 2014. Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest: Tree diversity promotes predator ants. *Ecol. Entomol.* 39:637–47

135. Strauss SY, Cacho NI, Schwartz MW, Schwartz AC, Burns KC. 2015. Apparency revisited. *Entomol. Exp. Appl.* 157:74–85

136. Tack AJM, Gripenberg S, Roslin T. 2012. Cross-kingdom interactions matter: Fungal-mediated interactions structure an insect community on oak. *Ecol. Lett.* 15:177–85

137. Thaler JS. 2002. Effect of jasmonate-induced plant responses on the natural enemies of herbivores. *J. Anim. Ecol.* 71:141–50

138. Underwood N, Inouye BD, Hambäck PA. 2014. A conceptual framework for associational effects: When do neighbors matter and how would we know? *Q. Rev. Biol.* 89:1–19

139. Unsicker SB, Kunert G, Gershenzon J. 2009. Protective perfumes: the role of vegetative volatiles in plant defense against herbivores. *Curr. Opin. Plant Biol.* 12:479–85

140. Vehviläinen H, Koricheva J, Ruohomäki K. 2008. Effects of stand tree species composition and diversity on abundance of predator arthropods. *Oikos* 117:935–43

141. Vehviläinen H, Koricheva J, Ruohomäki K, Johansson T, Valkonen S. 2006. Effects of tree stand species composition on insect herbivory of silver birch in boreal forests. *Basic Appl. Ecol.* 7:1–11

142. Vet LEM, Dicke M. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* 37:147–72

143. Viechtbauer W. 2010. Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* 36:1–48

144. Visser JH. 1986. Host odor perception in phytophagous insects. *Annu. Rev. Entomol.* 31:121–44

145. Wang X-F, Liu J-F, Gao W-Q, Deng Y-P, Ni Y-Y, et al. 2016. Defense pattern of Chinese cork oak across latitudinal gradients: influences of ontogeny, herbivory, climate and soil nutrients. *Sci. Rep.* 6:27269

146. Werner EE, Hall DJ. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042–52

147. White JA, Whitham TG. 2000. Associational susceptibility of cottonwood to a box elder herbivore. *Ecology* 81:1795–803

148. Zhang Q-H, Schlyter F. 2004. Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. *Agric. For. Entomol.* 6:1–20

149. Zhang Q-H, Schlyter F. 2010. Inhibition of predator attraction to kairomones by non-host plant volatiles for herbivores: a bypass-trophic signal. *PLOS ONE* 5:e11063

150. Zhang Y, Chen HY, Reich PB. 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *J. Ecol.* 100:742–49