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LETTER

Tree diversity reduces herbivory by forest insects

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Abstract

Biodiversity loss from plant communities is often acknowledged to affect primary production but little is known about effects on herbivores. We conducted a meta-analysis of a worldwide data set of 119 studies to compare herbivory in single-species and mixed forests. This showed a significant reduction of herbivory in more diverse forests but this varied with the host specificity of insects. In diverse forests, herbivory by oligophagous species was virtually always reduced, whereas the response of polyphagous species was variable. Further analyses revealed that the composition of tree mixtures may be more important than species richness *per se* because diversity effects on herbivory were greater when mixed forests comprised taxonomically more distant tree species, and when the proportion of non-host trees was greater than that of host trees. These findings provide new support for the role of biodiversity in ecosystem functioning across trophic levels.

Keywords

Biodiversity, ecosystem functioning, forest, herbivory, insect, meta-analysis.

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INTRODUCTION

The loss of biodiversity, mainly due to human activities, is a major environmental concern (United Nations 1992; Balmford & Bond 2005). Due to the combined effects of deforestation, forest fragmentation, declining habitat quality and climate change (Saunders *et al.* 1991; Lindenmayer & Franklin 2002; Brook *et al.* 2003; Thomas *et al.* 2004), biodiversity loss is particularly serious in forests, which appear to harbour more than half of the known terrestrial plant and animal species (Hassan *et al.* 2005). Apart from concerns for the conservation of biodiversity, the unprecedented loss of species may have dramatic detrimental effects on the functioning of ecosystems (Hooper *et al.* 2005). Although the large number of species involved in ecosystem processes and the complexity of their interactions make it difficult to draw general conclusions, a consensus is emerging that both species richness and community composition are important for ecosystem functioning (Hooper *et al.* 2005). However, this debate has focused on evidence from grasslands or microbial communities (Naeem *et al.* 1994; Tilman 1996; McCann 2000; Loreau *et al.* 2001, 2002; Mittelbach *et al.* 2001; Tilman *et al.* 2001; Hooper *et al.* 2005), whereas limited attention has been given to more complex ecosystems such as forests (Pretzsch 2003; Vila *et al.* 2003). Recently, two reviews analysed biodiversity effects on ecosystem functioning but only two of 446 studies considered by Balvanera *et al.* (2006) and none of the 111 experiments reported by Cardinale *et al.* (2006) concerned forests.

Furthermore, most studies focused on the producer level and paid little or no attention to interactions among multiple trophic levels (e.g. Balvanera *et al.* 2006), which would be more representative of real ecosystems. This is critical because diversity at the consumer level can be positively or negatively related to primary production (Ives *et al.* 2005), which may lead to idiosyncratic responses of multitrophic ecosystems to biodiversity loss (Hooper *et al.* 2005). Better resource exploitation is considered to be a main driver that leads to the greater productivity of diverse plant communities (Tilman 1996; Loreau *et al.* 2001). The same principle is likely apply to herbivores, which would result in increased plant consumption (Mulder *et al.* 1999; Cardinale *et al.* 2006). Studies that assessed interactions among trophic levels also revealed contrasting relationships between food web complexity and stability, with higher diversity resulting in lower population stability (Tilman 1996; McGrady-Steed & Morin 2000; Fox & McGrady-Steed 2002) and higher total productivity (Petchey 2000; Aoki 2003; Hillebrand & Cardinale 2004; Balvanera *et al.* 2006).

There is an under-utilized body of evidence from studies on forest diversity and insect herbivory that is highly

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relevant to this debate. The notion that boreal forests, single-species plantation forests and other low-diversity forests are particularly susceptible to pest outbreaks is widely cited in textbooks (e.g. Begon *et al.* 1996; Speight & Wylie 2001). However, previous reviews suggest that the evidence for this is equivocal (Gibson & Jones 1977; Schwerdtfeger 1981; Barthod 1994; Koricheva *et al.* 2006). Furthermore, pest problems in forest monocultures are not necessarily related to their simplified composition but could also be caused by their even-aged structure or intensive silvicultural practices (Watt 1992).

Here, we present the results from meta-analyses of 119 studies that compared insect herbivory on the same tree species growing in either pure or mixed stands. Meta-analysis is a powerful method (Gurevitch & Hedges 1993) to conduct quantitative, objective reviews of numerous independent studies. Our objectives were (i) to test the relationship between tree species diversity and forest insect herbivory, (ii) to examine whether such a relationship depends on species richness *per se* or more on tree species composition and (iii) to test whether responses of insect herbivores to tree diversity may depend on key functional traits of insect species. Our meta-analyses confirm that, overall, there is indeed an inverse relationship between forest diversity and herbivory. This applied virtually to all cases involving oligophagous species, whereas the relationship was weak when polyphagous species were considered. The qualitative composition of tree mixtures (e.g. whether mixtures of tree species composed of more or less closely related species) and the proportion of host and non-host tree species were also important. These findings are important for our understanding of forest ecology and for practical aspects of managed forests.

METHODS

Data collection

We searched for suitable studies using on-line bibliographic databases such as ISI Web of Science and CAB Abstracts and cited references in relevant publications. Our literature search yielded 119 individual studies, derived from 38 publications published from 1966 to 2006 and involved 33 tree species and 33 herbivorous insect taxa (in five additional cases the herbivore was not named; Appendix 1). We included studies for the meta-analyses if they met two conditions: (i) damage from herbivorous insect species (101 cases) or their abundance (18 cases) on a particular tree species (subsequently referred to as the 'focus tree species') was compared in pure vs. mixed stands, in the same area and time period and (ii) the mean of the response variable (herbivory), a measure of the variance and the sample size were reported in the text or available via graphic digitization. We chose the pure stand as the control and the mixed stand as the treatment group. When results for a response variable were reported in the same paper for several insect species, data for each insect were included as an individual study. Likewise, when different tree mixtures, in terms of species composition or relative abundance, were compared to the pure stand treatment, data for each paired tree diversity comparison were included as individual studies. Results for several sampling dates were not used as replicates to calculate mean, variance and sample size values unless data were obtained in independent tree samples.

Meta-analyses

Analyses were carried out using METAWIN 2.0 software (Rosenberg *et al.* 2000). For each individual study an estimate of the magnitude of the treatment effect, Hedges' d effect size (eqn 1.1) was calculated as the difference between the mean herbivory magnitude of the experimental group ($\bar{X}^E$, mixed stand) and the control group ($\bar{X}^C$, pure stand) divided by the pooled standard deviation (S, eqn 1.2), and multiplied by a correction factor (J, eqn 1.3) that accounts for small sample sizes (Hedges & Olkin 1985).

$$d = j\frac{\bar{X}^E - \bar{X}^c}{S} \tag{1.1}$$

$$S = \sqrt{\frac{(N^E - 1)(S^E)^2 + (N^C - 1)(S^C)^2}{N^E + N^C - 2}} \tag{1.2}$$

$$J = 1 - \frac{3}{4(N^C + N^E - 2) - 1} \tag{1.3}$$

A negative value of d indicates lower herbivory in mixed stands than in pure stands. Effect sizes across all studies were combined using the random effects model (Gurevitch & Hedges 1993) to provide the grand mean effect size (d_{++}). The effect was considered as statistically significant if the bootstrap confidence interval, calculated with 999 iterations, did not bracket zero. The so-called 'file drawer problem', which refers to the potential publication bias resulting from the greater likelihood of studies with statistically significant results being published than studies that did not show any significant effects, was addressed by calculating a fail-safe sample size which represents an estimate of the number of non-significant, unpublished or missing studies that would need to be added to the analysis in order to make the overall test of an effect statistically non-significant. Rosenthal's method was used to calculate the fail-safe number for our data set and this number was then compared to Rosenthal's (1979) conservative critical value of $5n + 10$, where n is the sample size.

Because effect sizes were significantly heterogeneous (Q-statistics) we split the data set into subsets of classes of different categories of insects and forest stand composition. Herbivorous insects were classified according to their host specificity, whereby those that are host specific to trees within a genus or a family were categorized as 'oligophagous' and those that feed on trees from more than one family as 'polyphagous'. Forests were classified according to the focus tree class (broadleaf vs. conifer). The tree species composition of mixed stands was classified according to the presence of other palatable host species for polyphagous insect herbivores (no host vs. less palatable host vs. more palatable host). The mean effect size (d_+) and a bootstrap confidence interval were then calculated for each class and the between-classes heterogeneity was tested against a chi-square distribution to evaluate the significance of the class effect. Because multiple tests were conducted with the same data set, the resulting P-value was assessed against a Bonferroni-adjusted alpha level, a method previously used with meta-analyses (e.g. Etzel & Guerra 2002). We split the data into two subpopulations (polyphagous and oligophagous insects), and tested the effects of two factors on each subpopulation, giving four separate tests in all and a conservative adjusted alpha of 0.0125 (alpha = 0.05/4).

To examine the effects on herbivory of the relative proportion of the associated tree species, the composition of mixed stands was classified as 'fewer or as many (≤ 50%)' vs. 'more (> 50%) associated trees than trees of the focus species' and herbivory in both types of mixed stands was compared with herbivory in the pure stands. This was possible with 24 studies involving oligophagous insects. A Wilcoxon paired test was used to compare Hedges' effect sizes calculated for the two combinations (pure stand and mixed stand with > 50% associated trees) vs. (pure stand and mixed stand with ≤ 50% associated trees). Furthermore, in eight case studies with oligophagous insect herbivores, the pure stand treatment was compared with several mixed stand treatments with an increasing proportion of associated tree species. We correlated Hedges' effect size for each comparison (pure stand vs. mixed stand) with the proportion of associated tree species in the corresponding mixed stand. The correlation coefficient r of individual studies was transformed to z correlations (Cooper & Hedges 1994) and the conditional variance of z was calculated using the METAWIN software. These estimates were included in a random model to test whether the overall mean of the correlations between the Hedges' effect size and the proportion of associated trees differed from zero. To facilitate the interpretation, the results (overall mean z) are presented as back-transformed correlation coefficients. The overall average coefficient r was analysed by calculating the 95% bootstrap confidence interval, as outlined in the text.

RESULTS

Our meta-analysis revealed that in forests of single tree species these species are significantly more affected by herbivory than the same species in more diverse forests (Table 1). The overall mean effect size equalled −0.67 and was significantly different from zero ($P = 0.0004$). According to Cohen (1988), an effect size of 0.5–0.8 shows a medium effect (as in this case) and an effect size > 0.8 shows a large effect. The fail-safe sample size was 3320, thus much greater than the conservative critical value of 605 ($5 \times 119 + 10$) and *c.* 28 times the number of studies included in the meta-analysis. Thus, this result is unlikely to be affected by the 'file drawer problem'.

For 115 of the 119 individual studies we were able to qualify the host specificity of the insect herbivore that was involved (Appendix 1). For oligophagous herbivores, there was a significant large and negative mean effect size, whereas for polyphagous insects, this was low and only marginally significant (Table 1). The difference between oligophagous and polyphagous insects was striking (Fig. 1) and highly significant (d.f. = 2, $Q_B = 11.5$, $P = 0.002$). (Note, for this and all following significance tests within this meta-analysis we used a Bonferroni-adjusted alpha level of 0.0125, as explained in the Methods.) Because of this dramatic difference, subsequent tests on the effects of additional variables on the diversity–herbivory relationship were conducted separately for oligophagous and polyphagous insect herbivores.

The qualitative composition of mixed stands had a significant overall effect for oligophagous insects. There was a consistently greater effect when the focus tree species and the associated tree species did not belong to the same class (i.e. broadleaved tree or conifer), with a mean effect size more than twice that for studies with mixtures that involved tree species from the same class (Table 1; d.f. = 1, $Q_B = 9.1$, $P = 0.004$). In contrast, for polyphagous insects there was no clear overall effect of the composition of mixed stands (Table 1; d.f. = 1, $Q_B = 0.7$, $P = 0.45$), although mixtures of trees from different classes had a marginally significant effect size, whereas the effect was not significant when mixtures comprised trees from the same class (Table 1).

Tests for the response in herbivory to the presence of other palatable host tree species in mixed stands also provided contrasting results for the oligophagous vs. polyphagous insect groups. Oligophagous insects showed a consistent reduction in herbivory in mixed stands regardless of the palatability of the other tree species (Table 1), although the effect size appeared to be somewhat larger when the associated trees were not palatable (d.f. = 1, $Q_B = 2.5$, $P = 0.10$). However, in studies involving polyphagous insects, the palatability of associated tree

Table 1 Meta-analyses of the influence of forest diversity on insect herbivory

Class variable*	Class	Sample size	Mean Hedges' effect size (d_+)†	Bootstrap confidence interval
All insects				
Overall		119	−0.67*	−0.86 to −0.49
Insect host specificity ($P = 0.002$)	Oligophagous‡	73	−0.95*	−1.19 to −0.75
	Polyphagous §	42	−0.34*	−0.62 to −0.06
Oligophagous insects ($n = 73$)				
Qualitative composition of mixed stands¶	Same classes (B + B or C + C)	36	−0.62*	−0.89 to −0.41
(associated + focus tree; $P = 0.004$**)	Different classes (B + C or C + B)	37	−1.33*	−1.69 to −0.98
Functional composition of mixed stands	No other palatable tree species	48	−1.11*	−1.44 to −0.82
[$P = 0.10$ (n.s.)]	Other less palatable tree species	23	−0.70*	−0.98 to −0.45
Polyphagous insects ($n = 42$)				
Qualitative composition of mixed stands	Same classes (B + B or C + C)	25	−0.25	−0.62 to +0.10
[associated + focus tree; $P = 0.45$ (n.s.)]	Different classes (B + C or C + B)	17	−0.47*	−0.86 to −0.04
Functional composition of mixed stands	No other palatable tree species	5	−1.61*	−2.62 to −0.61
($P = 0.001$**)	Other less palatable tree species	16	−0.66*	−0.91 to −0.46
	Other more palatable tree species	21	+0.16	−0.27 to +0.63

Herbivory is compared between pure stands of a focus tree species and mixed stands composed of the focus species and associated tree species. Negative Hedges' effect size indicates that the rate of herbivory on focus trees decreased in mixed stands.
*Class effect (*P*-value).
†The asterisk denotes a significant effect based on a bootstrap test.
‡Insects with a host range that includes at most one family of trees.
§Insects with a host range that includes trees from more than one family of trees.
¶Tree class: B = broadleaf, C = conifer.
**Significant if $P < 0.0125$ (Bonferroni correction, $\alpha = 0.05/4 = 0.0125$).

species was a significant factor (Table 1; d.f. = 2, $Q_B = 18.5$, $P = 0.001$). For the individual studies where no other palatable trees ($n = 5$) or only less susceptible tree species ($n = 16$) were present in mixed stands, the size of the overall effect was large or medium and negative, indicating that these mixed forests had a lower risk of damage from polyphagous pests (Table 1). On the other hand, for the other 21 studies where more palatable trees were present in mixed stands the overall effect size was positive, although non-significant (Table 1). This indicates that there is a risk of greater damage from polyphagous pests when a more palatable host tree is associated with the focus tree species (Table 1).

We were also able to examine the effects of different proportions of associated tree species in the mixed stands. We compiled a subset of studies that met this requirement, all concerning oligophagous insects, and compared the mean effect sizes of 24 pairs of individual studies focusing on the same insect–tree interaction where the proportion of associated tree species in the mixture was either greater than, equal to or smaller than the proportion of the focus tree species (Fig. 2). In studies where the proportion of associated tree species was > 50%, the mean effect size was on average approximately twice that (−2.7 vs. −1.2) of studies with a smaller proportion (Wilcoxon paired test, $n = 24$, $Z = 4.14$, $P < 0.0001$). This indicated that an increased proportion of associated trees in mixed stands led to a decrease in herbivory sustained by the focus trees (Fig. 2). This pattern was even more obvious in eight case studies with oligophagous insect herbivores where the pure stand treatment was compared with several mixed stand treatments with an increasing proportion of associated tree species. Overall, there was a consistently increasing effect size when the proportion of associated tree species increased (Fig. 3). The mean correlation coefficient r between the decrease in herbivory in mixed stands compared to pure stands and the rate of associated tree species was 0.95 and significantly different from 0 (95% bootstrap confidence interval ± 0.02; back-transformed from z-transformed correlation for random model).

DISCUSSION

Based on the evidence from 119 comparative studies of 47 different insect–tree interactions, our quantitative review showed that overall tree species growing in mixtures suffer significantly less herbivory than those in pure stands. This diversity effect on herbivory appears to be generally applicable at this forest stand scale as the studies used in our meta-analysis include a wide range of insect taxa and

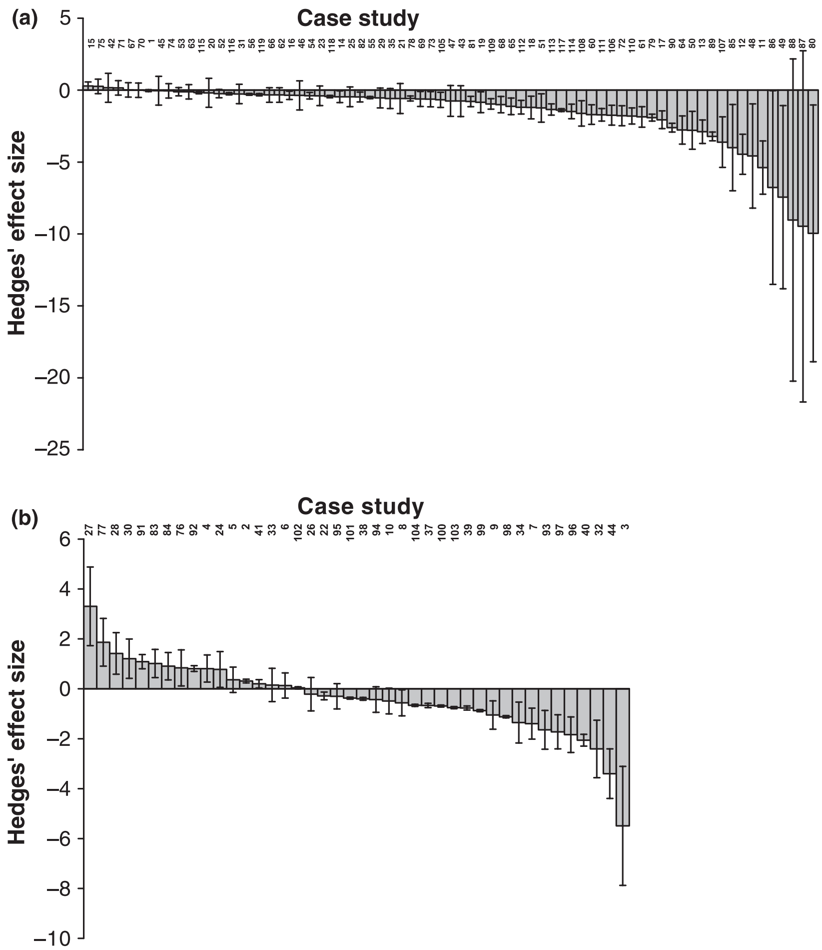

Figure 1 Hedges' *d* effect size and variance of individual studies on the response of forest insect herbivory to pure vs. mixed tree stand composition, for (a) oligophagous herbivores and (b) polyphagous herbivores. Negative effect sizes indicate that higher tree species diversity (mixed stand treatment) results in lower insect herbivore abundance or damage. More information on each study is given in Appendix 1.

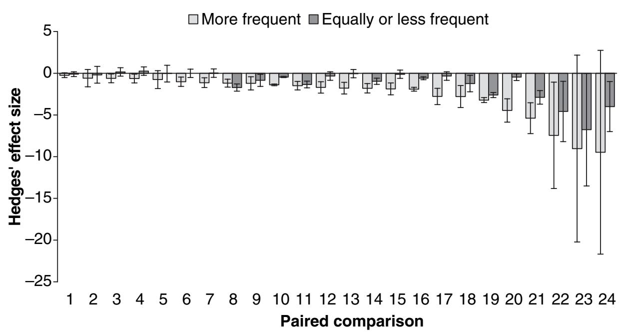

Figure 2 Twenty-four paired comparisons of the effect of increased tree species diversity on herbivory by oligophagous insects in mixed stands, in studies where two relative abundance classes of associated trees were compared with pure stands. Note: Light grey bars show Hedges' *d* effect size of insect herbivory in pure stands vs. mixed stands where associated trees were more frequent (> 50%) than the focus tree species. Dark grey bars show Hedges' *d* effect size of insect herbivory in pure stand vs. mixed stand where associated trees were less frequent (≤ 50%) than the focus tree species.

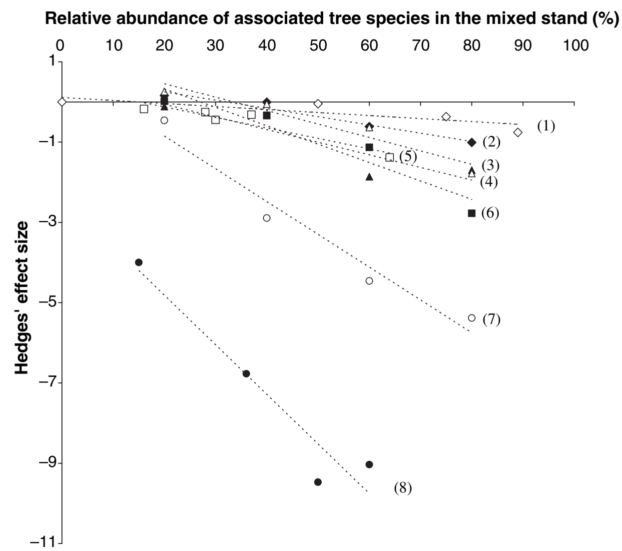

Figure 3 Eight response patterns of Hedges' *d* to the relative abundance of associated tree species in mixed stands compared with pure stands. (1) Nichols *et al.* 1999; (2, 4, 5, 6) Fauss & Pierce 1969; (3) Jactel *et al.* 2006; (7) Su *et al.* 1996; (8) Katovich 1992.

feeding guilds that affect trees from numerous plant families and orders in boreal, temperate and tropical biomes (see also Jactel *et al.* 2005). Overall, our study provides new and convincing support for the theory that species diversity of producer assemblages may reduce the magnitude of consumer effects on producers. Three similar meta-analyses that examined diversity effects in crop plant and algal communities (Tonhasca & Byrne 1994; Hillebrand & Cardinale 2004; Balvanera *et al.* 2006) also showed that more diverse communities were less affected by herbivore consumption. Our analysis gives support to the extension of this global pattern to long-lived producers such as tree species. However, the magnitude of this effect varied greatly in relation to an additional important factor that has been overlooked in previous studies, the host specificity of the primary consumer. The contrast between the responses of oligophagous and polyphagous herbivores to increased tree diversity was striking and merits further exploration.

What distinguished the subpopulation of studies involving *polyphagous* insects in our meta-analysis was the significantly different effect size in those studies where other, more palatable species were present in mixed stands. In at least six of these studies (Brown *et al.* 1988; Gottschalk & Twery 1989; White & Whitham 2000) this result can most likely be attributed to 'associational susceptibility', an outcome of the occurrence of several host tree species in situations where polyphagous herbivores may be able to use a more palatable host to build up their populations, exploit those resources and then 'spill over' to the associated hosts (Brown & Ewel 1987; White & Whitham 2000). For example, gypsy moth (*Lymantria dispar*) can feed on conifers once its preferred hosts, oaks and other broadleaved species have been defoliated. As a result of this polyphagy, white pine growing in mixed stands with oaks is more likely to be attacked by *L. dispar* than white pine in pure stands (Brown *et al.* 1988). We were able to confirm this process as a general pattern by separating studies with polyphagous insects according to the presence or absence of other host tree species in the mixture. Our results clearly showed that such a detrimental effect of tree diversity is not uncommon but only when a more palatable host is present in the tree species assemblage. Similar effects may apply to generalist mammalian grazers which appear to prefer mixed stands in boreal forests (Koricheva *et al.* 2006).

It is noteworthy that our analysis considers the *overall* effects of many different studies of which each examined a particular herbivore species on a particular focus tree species growing either in a pure or a mixed stand. It is conceivable that the observed *overall* reduction in herbivory by a particular oligophagous herbivore on a particular tree species could be outweighed by a corresponding *overall* increase in total herbivory by polyphagous species on all tree species present in mixed stands. To our knowledge, there has been no published study that specifically addressed this question in forest ecosystems; however, two observations can be offered that oppose this view: (i) collectively, overall herbivory by polyphagous species was not greater in mixed stands than in pure stands and (ii) oligophagous, i.e. specialist herbivores, are likely to exert a higher herbivory pressure than generalist, i.e. polyphagous species. This has been demonstrated particularly in tropical forests (Barone 1998, 2000).

In the subset of studies involving *oligophagous* insects, we observed a significant effect of the composition of mixed stands. Increased host availability is often cited as the main reason for the higher rates of herbivory in monocultures (Root 1973; Risch 1981; Russell 1989; Jones 2001). This process is well supported by the results of our meta-analyses which showed that trees in mixed stands consistently experienced less herbivory when the proportion of non-host trees increased (e.g. Fauss & Pierce 1969; Katovich 1992; Su *et al.* 1996; Nichols *et al.* 1999; Jactel *et al.* 2006). In more diverse plant communities, each particular plant species is relatively less abundant and its distribution is likely to be more patchy, making it less available to specialist herbivores (Kareiva 1983; Yamamura 2002). Apart from this 'spatial concentration' effect, an association with non-host species can also provide physical or chemical barriers to host location by foraging or dispersing herbivores. Numerous tree-feeding insects are wind-dispersed, and physical barriers are known to affect such insects in particular. For example, the larvae of *C. fumiferana* are passively dispersed by ballooning in wind currents, and their survival is higher in pure stands of balsam fir, their main host tree, than in mixed stands due to the reduced risk of landing on a non-host (Kemp & Simmons 1979). Hence, balsam fir in pure stands tends to be more defoliated than in mixed stands (Cappucino *et al.* 1998). Chemical barriers to host location are known to occur when stimuli from non-host trees disrupt olfactory host tree recognition. Several non-host volatiles have been identified from angiosperm trees, which showed repellent effects in conifer-feeding bark beetles (Byers *et al.* 1998; Schlyter *et al.* 2000; Huber & Borden 2001; Jactel *et al.* 2001; Zhang *et al.* 2001). Our analysis supports the relevance of this 'chemical barrier' effect on herbivory because associations of trees from two different classes (broadleaved trees and conifers) reduced herbivory in mixed stands more than associations of trees from the same class (e.g. broadleaved plus broadleaved or conifers plus conifers), which would have volatiles that are more similar.

Another likely mechanism is generally known as the 'natural enemy' hypothesis (Root 1973; Wilby & Thomas 2002; Cardinale *et al.* 2003; Jakel & Roth 2005; Riihimaki *et al.* 2005) but only a few of the studies included in our meta-analysis tested this directly. The density of accompanying understorey vegetation appeared not to influence the rate of parasitism of the Nantucket pine tip (Miller & Stephen 1983). In contrast, both Bae *et al.* (1997) and Quayle *et al.* (2003) showed that the parasitism rate of herbivorous insects was significantly higher in mixed stands than in pure stands. *Trichogramma minutum* Riley, the main parasitoid in a study on spruce budworm (*Choristoneura fumiferana*), is a generalist species that appeared to benefit from eggs of other insect species feeding on non-host trees (Quayle *et al.* 2003). Generalist parasitoids and predators are likely to encounter a higher availability of alternative prey or hosts in mixed forests because diverse plant communities usually provide habitat for more herbivorous species (Lawton & Strong 1981; Siemann *et al.* 1998). Richer plant communities can also provide a better supply of complementary food such as pollen, nectar and honeydew that improve the fitness of specialized parasitoids (Simmons *et al.* 1975; Russell 1989; Cappucino *et al.* 1999). Finally, because of their higher structural complexity, mixed forests may provide natural enemies with more opportunities to shelter from adverse conditions, or provide nesting sites as in the case of birds that prey on spruce budworm (Zach & Falls 1975; Dickson 1979).

Thus, our results are consistent with two of the main points in relation to the effects of biodiversity on ecosystem functioning on which ecologists recently agreed (Hooper *et al.* 2005): (i) species composition can be more important than species richness *per se* and (ii) the strength or the sign of the relationship can vary with the functional traits of the species. Our results confirm this because (i) the beneficial effects of tree diversity on herbivory increase with the relative proportion of associated trees, (ii) the association of phylogenetically less similar tree species, e.g. angiosperms associated with gymnosperms, is more effective in preventing herbivory in mixed stands and (iii) the association of more palatable host trees is likely to increase damage from polyphagous herbivores in the mixture. These findings also highlight the fact that insufficient consideration of such factors may lead to erroneous conclusions about the existence of such effects of biodiversity, and whether or not they are widely applicable. This also has important implications for the sustainable management of forests, particularly planted forests which are predominantly managed as monocultures and are expected to soon supply the majority of the world's demand for wood and fibre products (FAO 2001). Enhancing biodiversity by enriching forests with additional tree species that are less palatable for pest insects may increase food web stability while at the same time potentially offering conservation benefits. However, more comprehensive studies are needed to determine whether there is a concomitant effect of forest diversity on herbivory, productivity and conservation.

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Appendix 1 Summary of data included in the meta-analyses

Individual study	Authors	Tree species	Insect species	Insect host specificity	RAH*	Hedges' *d*	N^E	X^E	N^C	X^C	S
1	Su *et al.* (1996)	*Abies balsamea*	*Choristoneura fumiferana*	O	**More**	−5.38	5	0.14	5	0.72	0.10
2	Su *et al.* (1996)	*Abies balsamea*	*Choristoneura fumiferana*	O	**More**	−4.46	5	0.25	5	0.72	0.10
3	Su *et al.* (1996)	*Abies balsamea*	*Choristoneura fumiferana*	O	**Equal**	−2.89	5	0.32	5	0.72	0.12
4	Su *et al.* (1996)	*Abies balsamea*	*Choristoneura fumiferana*	O	**Less**	−0.46	5	0.65	5	0.72	0.13
5	Bergeron *et al.* (1995)	*Abies balsamea*	*Choristoneura fumiferana*	O	More	−1.21	3	57.57	3	74.00	10.87
6	Bergeron *et al.* (1995)	*Abies balsamea*	*Choristoneura fumiferana*	O	Less	−0.84	3	63.20	3	74.00	10.25
7	McLean (1980)	*Abies balsamea*	*Choristoneura fumiferana*	O		−0.39	3	0.27	3	0.37	0.21
8	Batzer *et al.* (1987)	*Abies balsamea*	*Choristoneura fumiferana*	O	More	−3.22	15	20.00	15	93.00	22.08
9	Batzer *et al.* (1987)	*Abies balsamea*	*Choristoneura fumiferana*	O	Less	−2.61	10	32.00	15	93.00	22.58
10	Quayle *et al.* (2003)	*Abies balsamea*	*Choristoneura fumiferana*	O		−0.67	4	0.25	4	0.33	0.11
11	Quayle *et al.* (2003)	*Abies balsamea*	*Choristoneura fumiferana*	O		−1.75	4	0.16	4	0.33	0.09
12	Montagnini *et al.* (1995)	*Albizia guachapele*	*Atta cephalotes*	P		0.13	4	0.71	4	0.70	0.04
13	Vehviläinen *et al.* (2006)	*Betula pendula*	Insect defoliators	O	Equal	−0.96	8	0.82	5	1.00	0.17
14	Vehviläinen *et al.* (2006)	*Betula pendula*	Insect defoliators	O	More	−1.80	5	0.68	5	1.00	0.16
15	Vehviläinen *et al.* (2006)	*Betula pendula*	*Acalitus rudis*	O	Equal	−1.72	8	1.96	5	4.29	1.26
16	Vehviläinen *et al.* (2006)	*Betula pendula*	*Acalitus rudis*	O	More	−1.19	5	2.50	5	4.29	1.36
17	Vehviläinen *et al.* (2006)	*Betula pendula*	Leaf rollers	O	Equal	−1.35	8	0.36	5	0.54	0.12
18	Vehviläinen *et al.* (2006)	*Betula pendula*	Leaf rollers	O	More	−1.48	5	0.36	5	0.54	0.11
19	Montagnini *et al.* (1995)	*Callophylum brasiliense*	*Atta cephalotes*	P		0.36	4	0.15	4	0.14	0.03
20	Brown & Ewel (1987)	*Cordia alliodora*	?	?		0.93	20	5.10	180	2.10	3.20
21	Gantner (2000)	*Corylus avellana*	*Myzocallis coryli*	O		−0.52	28	3.25	28	8.88	10.65
22	Montagnini *et al.* (1995)	*Dipteryx panamensis*	*Atta cephalotes*	P		−0.56	4	0.10	4	0.12	0.02
23	Smith *et al.* (1989)	*Eucalyptus botryoides*	*Cardiaspina fiscella*	O		−9.96	3	17.70	3	81.30	5.11
24	Zanuncio *et al.* (1998)	*Eucalyptus cloeziana*	*Lepidoptera* sp.	O		−2.06	5	1136.84	5	3326.32	959.35
25	Bigger (1985)	*Eucalyptus deglupta*	*Amblypelta cocophaga*	P		−0.28	13	0.33	13	0.41	0.25
26	Greaves (1966)	*Eucalyptus regnans*	*Chrysopthartha bimaculata*	O	Equal	−0.19	2	7.00	2	9.25	6.83
27	Greaves (1966)	*Eucalyptus regnans*	*Chrysopthartha bimaculata*	O	More	−0.59	2	3.90	2	9.25	5.20
28	Montagnini *et al.* (1995)	*Genipa americana*	*Atta cephalotes*	P		−1.05	4	0.07	4	0.09	0.02
29	Nichols *et al.* (1999)	*Milicia excelsa*	*Phytolyma lata*	O	**Equal**	−0.04	2	11.36	2	12.26	11.91
30	Nichols *et al.* (1999)	*Milicia excelsa*	*Phytolyma lata*	O	**More**	−0.37	2	6.69	2	12.26	8.71
31	Nichols *et al.* (1999)	*Milicia excelsa*	*Phytolyma lata*	O	**More**	−0.76	2	2.86	2	12.26	7.09
32	Petersson & Örlander (2003)	*Picea abies*	*Hylobius abietis*	P		−0.43	4	10.15	4	17.60	15.06
33	Petersson & Örlander (2003)	*Picea abies*	*Hylobius abietis*	P		−0.30	4	3.35	4	5.08	5.01
34	Örlander *et al.* (2001)	*Picea abies*	*Hylobius abietis*	P		−1.84	4	54.00	4	140.00	40.73
35	Örlander *et al.* (2001)	*Picea abies*	*Hylobius abietis*	P		−1.72	4	67.30	4	82.10	7.47
36	Nordlander *et al.* (2003)	*Picea abies*	*Hylobius abietis*	P		−1.12	50	4.16	50	9.04	4.33
37	Nordlander *et al.* (2003)	*Picea abies*	*Hylobius abietis*	P		−0.87	50	3.22	50	6.41	3.63
38	Nordlander *et al.* (2003)	*Picea abies*	*Hylobius abietis*	P		−0.69	50	0.94	50	2.62	2.42
39	Nordlander *et al.* (2003)	*Picea abies*	*Hylobius abietis*	P		−0.37	50	3.63	50	4.96	3.54

Appendix 1 (*Continued*)

Individual study	Authors	Tree species	Insect species	Insect host specificity	RAH*	Hedges' d	N^E	X^E	N^C	X^C	S
40	Nordlander *et al.* (2003)	*Picea abies*	*Hylobius abietis*	P		0.04	50	3.08	50	2.96	2.87
41	Nordlander *et al.* (2003)	*Picea abies*	*Hylobius abietis*	P		−0.76	50	0.55	50	2.00	1.90
42	Nordlander *et al.* (2003)	*Picea abies*	*Hylobius abietis*	P		−0.66	50	3.85	50	6.07	3.33
43	Taylor *et al.* (1996)	*Picea glauca*	*Pissodes strobi*	O	More	−2.79	3	6.78	3	18.34	3.31
44	Taylor *et al.* (1996)	*Picea glauca*	*Pissodes strobi*	O	Equal	−1.24	2	12.65	3	18.34	3.34
45	McLean (1989)	*Picea sitchensis*	*Pissodes strobi*	O		−0.79	6	5.33	6	17.00	13.58
46	McLean (1989)	*Picea sitchensis*	*Pissodes strobi*	O		−0.48	6	2.00	6	9.33	14.10
47	Bae *et al.* (1997)	*Pinus densiflora*	*Thecodiplosis japonensis*	O		−0.29	30	39.45	30	44.75	18.06
48	Bae *et al.* (1997)	*Pinus densiflora*	Mite	?		−0.78	4	1.14	4	2.00	0.96
49	Bae *et al.* (1997)	*Pinus densiflora*	Scale insect	?		0.19	4	0.36	4	0.31	0.23
50	Bae *et al.* (1997)	*Pinus densiflora*	Leaf aphid	?		−0.53	4	0.21	4	0.39	0.29
51	Géri (1980)	*Pinus nigra laricio*	*Thaumetopoea pytiocampa*	O	Equal	−0.59	10	0.84	15	1.29	0.73
52	Géri (1980)	*Pinus nigra laricio*	*Thaumetopoea pytiocampa*	O	More	−1.91	10	0.05	15	1.29	0.63
53	Jactel *et al.* (2006)	*Pinus pinaster*	*Matsucoccus feytaudi*	O	**Less**	−0.18	25	10.68	25	13.16	13.91
54	Jactel *et al.* (2006)	*Pinus pinaster*	*Matsucoccus feytaudi*	O	**Less**	−0.26	25	15.32	25	18.84	13.53
55	Jactel *et al.* (2006)	*Pinus pinaster*	*Matsucoccus feytaudi*	O	**More**	−1.39	25	0.24	25	19.80	13.90
56	Jactel *et al.* (2006)	*Pinus pinaster*	*Matsucoccus feytaudi*	O	**Less**	−0.45	25	17.64	25	25.28	16.82
57	Jactel *et al.* (2006)	*Pinus pinaster*	*Matsucoccus feytaudi*	O	**Less**	−0.32	25	12.32	25	18.08	17.93
58	Gottschalk & Twery (1989)	*Pinus strobus*	*Lymantria dispar*	P		0.84	3	0.59	3	0.28	0.29
59	Gottschalk & Twery (1989)	*Pinus strobus*	*Lymantria dispar*	P		1.87	3	0.80	3	0.28	0.22
60	Brown *et al.* (1988)	*Pinus strobus*	*Lymantria dispar*	P		1.02	4	48.13	4	17.18	26.50
61	Brown *et al.* (1988)	*Pinus strobus*	*Lymantria dispar*	P		0.91	4	48.80	4	17.18	30.34
62	Katovich (1992)	*Pinus strobus*	*Pissodes strobi*	O	**Less**	−4.00	2	37.80	2	68.70	4.41
63	Katovich (1992)	*Pinus strobus*	*Pissodes strobi*	O	**Less**	−6.77	2	15.40	2	68.70	4.50
64	Katovich (1992)	*Pinus strobus*	*Pissodes strobi*	O	**Equal**	−9.47	2	5.70	2	68.70	3.80
65	Katovich (1992)	*Pinus strobus*	*Pissodes strobi*	O	**More**	−9.03	2	4.20	2	68.70	4.08
66	Stadniskii (1978)	*Pinus sylvestris*	*Hylobius abietis*	P		−3.40	4	0.24	6	0.68	0.12
67	Von Sydow & Örlander (1994)	*Pinus sylvestris*	*Hylobius abietis*	P		−1.64	3	13.16	4	57.89	22.94
68	Schowalter & Turchin (1993)	*Pinus taeda*	*Dendroctonus frontalis*	O		0.16	2	1.00	2	0.80	0.71
69	Schowalter & Turchin (1993)	*Pinus taeda*	*Dendroctonus frontalis*	O		−0.76	2	0.80	2	5.50	3.54
70	Miller & Stephen (1983)	*Pinus taeda*	*Rhyacionia frustrana*	O	More	−0.24	7	13.65	7	18.70	19.38
71	Miller & Stephen (1983)	*Pinus taeda*	*Rhyacionia frustrana*	O	Equal	−0.11	7	15.99	7	18.70	22.37
72	Berisford & Kulman (1967)	*Pinus taeda*	*Rhyacionia frustrana*	O		−0.39	9	36.33	9	43.56	17.77
73	Nowak *et al.* (2003)	*Pinus taeda*	*Rhyacionia frustrana*	O		−3.62	3	21.00	3	50.70	6.56
74	Nowak *et al.* (2003)	*Pinus taeda*	*Rhyacionia frustrana*	O		−1.62	3	37.10	3	50.60	6.68
75	White & Whitham (2000)	*Populus angustifolia*	*Alsophila pometaria*	P		1.09	8	32.00	8	13.00	16.49
76	White & Whitham (2000)	*Populus angustifolia*	*Alsophila pometaria*	P		0.81	19	48.00	19	26.00	26.51
77	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**More**	−1.70	4	34.90	4	60.83	13.26
78	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**More**	−1.86	4	39.35	4	60.83	10.03

Appendix 1 (*Continued*)

Individual study	Authors	Tree species	Insect species	Insect host specificity	RAH*	Hedges' *d*	N^E	X^E	N^C	X^C	S
79	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**Equal**	−0.34	4	57.28	4	60.83	9.17
80	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**Less**	−0.11	4	59.48	4	60.83	10.33
81	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**More**	−2.77	4	8.08	4	42.75	10.88
82	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**More**	−1.13	4	24.20	4	42.75	14.28
83	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**Equal**	−0.33	4	37.50	4	42.75	13.63
84	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**Less**	0.02	4	43.00	4	42.75	12.22
85	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**More**	−1.01	4	41.70	4	61.95	17.44
86	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**More**	−0.61	4	48.95	4	61.95	18.44
87	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**Equal**	0.00	4	61.85	4	61.95	17.91
88	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**Less**	0.16	4	65.10	4	61.95	17.18
89	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**More**	−1.78	4	19.70	4	57.65	18.53
90	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**More**	−0.63	4	40.60	4	57.65	23.42
91	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**Equal**	−0.05	4	56.55	4	57.65	19.54
92	Fauss & Pierce (1969)	*Pseudotsuga menziesii*	*Choristoneura occidentalis*	O	**Less**	0.26	4	63.30	4	57.65	18.93
93	Moore *et al.* (1991)	*Quercus petraea*	*Phyllobius argentatus*	P		0.78	3	231.00	3	125.33	108.94
94	Moore *et al.* (1991)	*Quercus petraea*	?	O		−0.47	3	488.33	3	538.67	86.58
95	Moore *et al.* (1991)	*Quercus petraea*	*Phyllonorycter* spp.	P		−0.21	3	11.00	3	12.33	5.02
96	Moore *et al.* (1991)	*Quercus petraea*	*Stigmella* spp.	P		3.30	3	18.00	3	2.00	3.87
97	Moore *et al.* (1991)	*Quercus petraea*	?	P		1.42	3	345.00	3	68.67	155.91
98	Moore *et al.* (1991)	*Quercus petraea*	*Neuroterus* spp.	O		−0.54	3	0.74	3	3.19	3.63
99	Moore *et al.* (1991)	*Quercus petraea*	*Phyllobius argentatus*	P		1.21	3	295.67	3	125.33	113.07
100	Moore *et al.* (1991)	*Quercus petraea*	?	O		−0.27	3	500.33	3	538.67	114.20
101	Moore *et al.* (1991)	*Quercus petraea*	*Phyllonorycter* spp.	P		−2.41	3	1.00	3	12.33	3.76
102	Moore *et al.* (1991)	*Quercus petraea*	*Stigmella* spp.	P		0.15	3	2.67	3	2.00	3.49
103	Moore *et al.* (1991)	*Quercus petraea*	?	P		−1.35	3	21.33	3	68.67	28.00
104	Moore *et al.* (1991)	*Quercus petraea*	*Neuroterus* spp.	O		−0.58	3	0.52	3	3.19	3.66
105	Soria *et al.* (1995)	*Quercus rotundifolia*	*Curculio elephas*	O		0.28	7	11.61	7	9.20	7.98
106	Soria *et al.* (1995)	*Quercus suber*	*Curculio elephas*	O		−0.36	7	9.29	7	12.10	7.35
107	Wazihullah *et al.* (1996)	*Sonneratia apetala*	*Zeuzera conferta*	P		−0.67	20	15.00	29	27.00	17.66
108	Wazihullah *et al.* (1996)	*Sonneratia apetala*	*Zeuzera conferta*	P		−0.40	36	42.00	34	54.00	29.56
109	Wazihullah *et al.* (1996)	*Sonneratia apetala*	*Zeuzera conferta*	P		−0.77	31	32.00	24	51.00	24.40
110	Wazihullah *et al.* (1996)	*Sonneratia apetala*	*Zeuzera conferta*	P		−2.06	13	22.00	13	56.00	15.98
111	Wazihullah *et al.* (1996)	*Sonneratia apetala*	*Zeuzera conferta*	P		0.20	12	17.00	12	13.00	19.20
112	Folgarait *et al.* (1995)	*Stryphnodendron microstachyum*	*Cecidomyiidae* sp.	O		−0.03	80	0.14	16	0.15	0.24
113	Folgarait *et al.* (1995)	*Stryphnodendron microstachyum*	*Euclystis* sp.	P		0.31	80	0.02	16	0.01	0.02
114	Montagnini *et al.* (1995)	*Stryphnodendron microstachyum*	*Atta cephalotes*	P		−5.49	4	0.41	4	0.87	0.07
115	Keenan *et al.* (1995)	*Toona ciliata*	*Hypsipyla robusta*	O	Equal	−4.58	2	0.23	2	0.71	0.06
116	Keenan *et al.* (1995)	*Toona ciliata*	*Hypsipyla robusta*	O	More	−7.44	3	0.10	2	0.71	0.06
117	Montagnini *et al.* (1995)	*Virola koschnyi*	*Atta cephalotes*	P		−1.39	4	0.14	4	0.25	0.07

Appendix 1 (*Continued*)

Individual study	Authors	Tree species	Insect species	Insect host specificity	RAH*	Hedges' d	N^E	X^E	N^C	X^C	S
118	Montagnini *et al.* (1995)	*Vochysia ferruginea*	*Atta cephalotes*	P		−0.49	4	0.06	4	0.06	0.01
119	Montagnini *et al.* (1995)	*Vochysia guatemalensis*	*Atta cephalotes*	P		0.81	4	0.12	4	0.09	0.03

Insect host specificity: O for oligophagous, P for polyphagous; RAH: relative abundance of host tree species in the mixture; Hedges' *d*: Hedges' unbiased effect size of insect herbivory; N^E: sample size of the experimental group (mixed stand); X^E: mean value of the experimental group (mixed stand); N^C: sample size of the control group (pure stand); X^C: mean value of the control group (pure stand); S: pooled standard deviation.
*RAH in bold indicates the studies for which at least two levels of host tree abundance could be compared (see Fig. 2).